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STUDIES IN ROOT-PARASITISM.

IV—THE HAUSTORIUM OF CANSJERA RHEEDII.

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STUDIES IN ROOT-PARASITISM.

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THE HAUSTORIUM OF CANSJERA RHEEDII.

THERE is nothing in the appearance of *Cansjera Rheedii* which would lead one to suspect that it was a parasite. A large, scandent shrub, with whip-like branches, clothed with dark-green leaves and clusters of small whitish flowers, it is in no way remarkable among the multitude of tropical climbers around it. The stem frequently attains a considerable thickness, and the plant has some pretensions to beauty when covered with its bright red, oval berries. But our study of *Santalum album*, and especially of *Olax scandens*,* has taught us that, in the tropics, the parasitic habit may leave as little mark upon large shrubs and even trees as it does on the small, herbaceous, grass-feeding *Rhinanthaceæ* in Europe.

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* The following papers on the haustoria of *Santalaceæ* and *Olacaceæ* have recently been published by the author. As these papers will of necessity be frequently referred to, their titles will be abbreviated as follows :—

Sant. I and *II*—Studies in Root Parasitism. The Haustorium of *Santalum album*, Part I. Early Stages, up to Penetration. Part II. The Structure of the Mature Haustorium and the Inter-relations between Host and Parasite. Memoirs of the Department of Agriculture in India, Botanical Series, Vol. I, No. I, Parts I and II.

Olax—Studies in Root-Parasitism. The Haustorium of *Olax scandens*. Ibid. Vol. II. No. IV.

Par. Trees—Parasitic Trees in Southern India. Proceedings of the Cambridge Philosophical Society, Vol. XIV, Part III, read 20th May 1907.

To avoid unnecessary repetition, the various terms employed for the different parts of the haustorium in these papers will be adopted, as a rule, without explanation.

Cansjera Rheedii is widely distributed over India, being found at intervals from the northern parts of the Gangetic plain to Cape Comorin. It also occurs in Ceylon and China, and spreads across the Malay Archipelago to the tropical parts of Australia. In Madras it occupies a somewhat more elevated and inland position than *Olax scandens*, its native haunts being rather the hills of the Eastern Ghauts and the Deccan plateau than the Coromandel coast. The genus *Cansjera* is a small one, consisting of three or four species confined to the tropical parts of Asia and Australia.

As regards its systematic position, there is considerable divergence of opinion. In the Flora of British India it is placed among the *Opilieæ*, a sub-group of the *Olacaceæ*, but this arrangement can at best be regarded as only temporary. Recent studies on the anatomy of the *Olacaceæ* tend to separate that order, as defined in the F. B. I., into several perfectly distinct groups, and the *Opilieæ* are placed by Van Tieghem next to the *Santalaceæ*. This subject has been briefly referred to in a recent paper (*Par. Trees*), where it is shown that, judging by the structure of its haustorium, *Cansjera* is closely allied to the *Santalaceæ*, while its relationship with *Olax* is much more remote. The remarks on *Cansjera* made by King in his "Materials to the Flora of the Malay Peninsula" would thus appear to be justified from a study of its anatomy as well as by its other characters. He describes it as a "genus allied to *Champereia* which has already been transferred by Bentham and Hooker to *Santalaceæ*. It is also allied to *Lepionurus* and *Opiliea* and, with these, it should, in my opinion, be retransferred to the family *Santalaceæ* in which its founder Jussieu originally placed it." It will be of interest to study the roots of *Champereia* when obtainable. There would appear to be little doubt that it too is parasitic, not only from its close relationship with *Cansjera* and the *Santalaceæ*, but also from its reported appearance in the field.

Cansjera Rheedii affects much the same localities as *Santalum album* and *Olax scandens*: it is rare to find it isolated,

and it usually twines its scandent branches among the thickets of the scrub jungle. Its associates are indicated by the list in the appendix, which enumerates the plants whose connections with *Cansjera* have been studied in the preparation of the present paper.

2. The root-system of *Cansjera Rheedii* is, as might be expected, largely superficial. It is much branched and ends in small white rootlets. This is the description brought in by collectors, and I have not had the opportunity at present of making personal observations in the field. In the material collected the rootlets are practically devoid of root-hairs, while the young haustoria are somewhat densely clothed with them. From this it would appear that *Cansjera* resembles *Santalum* rather than *Olax* in the degree of its parasitism. (Plate I, fig. 1. *h. h.* See also *Sant. I*, 8, 9, and *Olax*, 5, 6.)

The haustoria are small and irregular, varying from 2 to 8 mm. in length. They are whitish in colour, even when very old, and more or less covered with warty excrescences. They are very different in appearance from those of *Santalum*, and this, it will be remembered, was the fortunate circumstance which led to the discovery of the parasitism of the plant (*Sant. I*, 1). In *Santalum* the older haustoria soon assume a brownish tinge, from the presence of a red-brown corky layer. The cork of *Cansjera* is yellowish, and the abundance of lenticels may, in the first instance, cause the surface to assume its warty appearance. Many of the older specimens are much distorted and form lobed masses in which it is difficult to determine the point of attachment to the host's root. This is very different from the limpet-like form of old Sandal haustoria (Plate I, figs. 1—7).

The material collected has not been altogether satisfactory, especially as regards the young stages, although several localities were tried at different times of the year. No seeds have been as yet obtainable, with the result that germination has not been followed.

3. Comparatively few young stages have been found in the numerous sections examined. In attempting to remedy this defect, a number of minute haustoria fixed to the roots of *Abrus precatorius* were imbedded in paraffin and cut with the microtome. But, unfortunately, some of the very smallest showed complete penetration, and most were fairly mature. The few cases of young haustoria met with show that the early stages have slight peculiarities which separate them both from *Olax* and *Santalum*, and it will, on that account, be necessary to describe the development of the haustorium.

No haustorium has been cut in which the nucleus is not already indicated. The earliest is a microtome section, and the cells are not altogether suited for the study of their contents. In this haustorium (Plate I, fig. 8), there is a median area of small cells in the act of rapid division, and around this the cells are arranged in definite order. This is the first appearance of the nucleus and the curves of growth in the ground tissue around it.

The haustorium is firmly attached to the root of the host (*Abrus precatorius*) and is fitted into all the unevennesses of its surface. This firm attachment of the haustorium to the objects it meets requires a moment's attention, as it does not seem to be merely a pressure phenomenon. It appears probable that a gummy substance is secreted, as in *Ampelopsis* or the climbing roots of ivy and pepper, but as yet no definite proof of the existence of such a substance has been obtained.

From a study of the tissues along the line of contact we learn several things. In the first place, a very distinct growing edge is distinguishable (as in *Santalum*) on each side of the haustorium. The haustorium is thus seen to be growing tangentially to the surface of the host's root. But, besides this growth at the edges, there is considerable increase in size in the middle part, resulting in a spreading movement of the tissues of the haustorium in contact with the root attacked. This is shown in the figure (8 *b*) by the doubling up of a piece of cork which is being rolled over in much the same manner as we

noted in our study of *Santalum album* (*Sant. II*, Plate V, fig. 2).

4. In the next stage of development considerable differentiation of tissues has taken place (Plate II, fig. 1). The sections were mounted in dilute glycerine, and it is thus possible to study the cell contents more carefully. The first point of importance is the presence of a well-marked hypodermal layer (*a*). This is characteristic of *Cansjera* haustoria. Starch, although sometimes present here, is hidden by dense granular contents which in later stages assume the form of oily (?) drops. Immediately within the hypoderm the cortex (*f*) becomes early cleared of contents and the deeper, starch-laden cells (*g*) are arranged much as in the earlier stages of the *Olax* haustorium (Olax, Plate III, fig. 2). The densest part of the shadow of starch grains is met with outside the upper part of the nucleus, and the tissues become clearer along the lines of growth towards the host's root. The lines of growth are well defined and the cortex is distinctly separable from the nucleus. The development of the vascular system is, as usual, the vessels in the transitional region appearing long before those lower down. A downward extension of the vascular system is also commencing on each side of the nucleus, the cells of these procambial strands being densely filled with protoplasm and actively dividing by longitudinal walls (*c*).

The upper limit of the nucleus is clearly shown at this early stage, in this respect differing markedly from the haustorium of *Olax*. The cells immediately above the nucleus (*b*), really ground tissue and therefore of a similar origin to those of the cortex, but separated from it by the procambial strands, have become elongated tangentially and form a distinct mass of tissue. The cells of the nucleus, on the other hand, remafn at first isodiametrical and divide rapidly in all directions (*d*).

In the lower part of the nucleus a median strand of tissue is traceable, the contents of whose cells become applied to their walls, giving them an appearance of thickening (*e*). This

median strand is continued almost to the surface of the host's root. It would appear that this is the first stage in the development of the gland.

5. In the next stage figured, the gland is already well formed (Plate II, fig. 2). The arrangement of the outer, clear and inner, starch-laden cells of the cortex closely resembles that in *Olax*, but the cell contents have not been drawn in the figure. At the line of separation between these two parts of the cortex, however, the collapsed layers are becoming apparent (*bb*). And here we meet with another marked disagreement with the course of development in *Olax*. The collapsed layers in *Cansjera* are developed like those in *Santalum*.

The curved lines of growth are well seen. The nucleus is sharply separated off from the tissue outside it, and the vascular loop is indicated. The portion of ground tissue above the nucleus and between the arms of the vascular loop has cells yet more elongated horizontally than in the preceding stage, and there is evidence of pressure from the expanding nucleus below.

In the lower part of the nucleus the gland is well seen. In the few examples obtained this organ is extremely simple in structure, consisting of a median split in the nuclear tissue, lined by secreting cells. The gland in *Cansjera* is totally different from that in *Olax*. It resembles that in *Santalum* in being lined by a well-marked epithelium, but it is doubtful whether a duct is present, as in that case. The lumen is narrow and uniform in all the cases met with. The glandular cells themselves are like those already described for *Santalum* (*Sant. I*, para. 14). They have a dense mass of granular protoplasm at the base, while the upper part of the cell is clear (fig. *a*). The secretion, formed in this upper part of the cell, exudes in granular mucilaginous rods which fill the cavity of the lumen. These rods are better shown in the section drawn on Plate III (fig. 2). In the horizontal section through a slightly older haustorium (fig. 1) the various tissues referred to above

may be followed. The hypoderm, clear and starch-laden cells of the cortex, the collapsed layers, the protoplasmic cells of the nucleus and the grandular epithelium are clearly separable.

6. Cases of haustoria in the act of entering the host's root are extremely rare. This fact was noted in both *Santalum* and *Olax*, and it was suggested that the cause was to be sought in the rapidity with which the sucker penetrates the cortex. Among the numerous sections of haustoria examined in the preparation of this paper, only one such case has been met with, and that is an exceedingly minute haustorium, less than one-sixteenth of an inch in diameter. The sections were cut with the microtome, stained with Delafield's hæmatoxylin and mounted in Canada balsam. They prove to be of much interest, and a detailed study of one of them is made on Plate IV.

In the transitional region the vascular strands are well seen, but no vessels are yet formed, and the strands are thus procambial (*a*, *e*). A distinct hypodermal layer is visible in the upper part of the haustorium, although its contents are not well shown. The cortical cells within it are devoid of contents with the exception of delicate protoplasmic sacs (*b*). The cells of the ground tissue in the vascular loop are sharply separated from the nucleus: they are, as usual, elongated horizontally and have well marked nuclei but little protoplasm (*c*). In the haustorium proper, below the transitional region, the collapsed layers are clearly shown, although still very thin. The cortical cells outside them (*h*) are moribund and empty and have merely a trace of protoplasm here and there. The cells of the inner cortex have distinct protoplasm and nuclei (*g*), but, from the mode of preparation, the distribution of the starch grains is not easy to make out. It is to be noted that the collapsed layers in *Cansjera* do not proceed down the whole length of the cortical folds. They turn inwards and terminate at a point half-way between the edge of the fold and the sucker. This is characteristic of *Cansjera* and forms another

distinction between its haustorium and those of *Olax* and *Santalum.*

The cortical folds have ceased to grow at their edges and a growing point can no longer be traced. But a well-marked group of cells is found in the thickness of the fold, whose walls have evidently undergone some change (*j*). These walls are not stained by hæmatoxylin and thus present a yellowish patch of tissue in the surrounding violet. The addition of anilin sulphate causes them to assume a bright yellow colour, with chloroiodide of zinc they turn brown and with phloroglucin and hydrochloric acid they become pink. These and other tests show them to be lignified. The walls are thickened and pitted and their presence in this region is typical of most *Cansjera* haustoria.

The nucleus, as might be expected from the important part played by it in penetration, shows the greatest changes. The cells in the upper part have enormously increased in size, so as to greatly exceed those of the ground tissue above them, and have become distinctly elongated in the direction of the sucker. They form a striking feature in all sections of haustoria at this stage, and have large nuclei and nucleoli imbedded in deeply staining granular protoplasm. Their cell-walls, on the other hand, are extremely thin and difficult to distinguish. The appearance of these nucleated cells is so remarkable that a question as to their function naturally arises. It does not seem sufficient to assign to them a merely nutritive or mechanical action in forcing the sucker downwards into the host. The cell contents are very like those of glandular organs. A study of the drawings in Plates IV and V (*d*', *d*, *a*, *a*', and *a*) will indicate successive stages in their development, and it may be noted that they appear most like glandular cells at the moment of penetration. We have seen that the nucleus of the haustorium in *Olax* is practically all taken up in the formation of the gland, and it appears probable that the same is the case, although in a different manner, in *Cansjera.* The slit-like "gland" (*e*) then assumes more the character of a duct, and the

figure on Plate IV supports this view. There is nothing of this in the haustorium of *Santalum*. Although the upper limit of the nucleus is quite sharp there, the cells are not thus enlarged, being little if any larger than those of the ground tissue above them (*Sant. II*, Plates I—III).

On either side of the nucleus the procambial strands are clearly visible; and their cells are dividing vertically only, so as to become elongated in this direction (*e*).

The lower part of the nucleus is divided into two parts, an outer (*f*), with small elongated nucleated cells, and a median strand with dense granular protoplasm, arranged as an epithelium on both sides of a narrow slit (*i*). This is presumably the gland in a late stage.

The young sucker is formed of the extension downwards of the lower part of the nucleus, and it has penetrated half-way through the host's cortex on its way to the vascular cylinder.

Details of all these tissues may be followed on Plate IV, where enlarged drawings are made of the cells in different regions.

7. The next stage, where the sucker has reached the woody cylinder of the host's root but has itself not yet formed vessels, is frequently met with, and is very characteristic of these haustoria (Plate V, fig. 1).

The cortical folds are assuming their permanent form. Growth in length has ceased, but a considerable thickening is noticeable on the inner side. Such growth in thickness, which is frequent in *Cansjera*, has not been noticed in either *Olax* or *Santalum*.

The collapsed layers are now much thicker, and separate the outer, empty cells of the cortex from the central, more or less protoplasmic mass. As before, the collapsed layers do not pass to the ends of the cortical folds, and abut on the host's bark half-way between the edge of the fold and the point where the sucker enters. The upper limit of the nucleus is particularly sharp, the cells of this region being, as usual, prominent.

As already noted, the cells of the nucleus are elongated in a direction at right angles to those immediately above them, and the latter are now considerably crushed by the nuclear growth.

The inner cortex is seen to have separated into two distinct parts. In the outer, the cells are more or less isodiametrical and filled with starch (*b*), while, in the inner, they are free from starch, have evident, nucleated protoplasm and are elongated in the direction of the sucker (*c*). This division of the inner cortex into two parts, although sometimes very clearly shown, is not always very definite. It calls to mind very forcibly the arrangement of tissues in the penetrating haustorium of *Olax scandens* (*Olax*, Plate VIII). In the latter case, however, the inner, elongating cells belong to the nucleus and the outer, starch-laden cells to the cortex. The sucker in *Olax* is formed entirely of nuclear tissue, whereas in *Cansjera*, as in *Santalum*, the sucker is formed chiefly of nucleus, but certain of the cortical cells take part, becoming greatly elongated and entering the split in the host's bark.

The sucker has reached the host's wood and is spreading along the cambial line on each side, thus becoming lobed. There is no trace of a former "gland," as in Plates III and IV, showing that the formation of this structure is not necessary for penetration. (See however para. 5.)

8. In Plate V, fig. 2, is shown a drawing of a mature haustorium penetrating a root of *Santalum album*. The main difference from the preceding stage lies in the development of the vascular system which is now fully formed. In the transitional region two strands are seen, interrupted at intervals by broad medullary rays and separated from the surrounding tissues by a distinctly marked endodermis (*e*). A well developed interrupted zone (*i. z.*) is seen at the top of the vascular loop, where the transitional region joins the haustorium proper. Below the interrupted zone the vascular loop is well defined, curving round to become a pair of strands in the haustorial axis, here without any trace of medullary rays. Two

continuous bands of vessels pass down the axis of the sucker, separated by a well-defined pith and clothed on their outer sides by cambium(*c*).

The cortex has undergone little change beyond its loss of contents. The collapsed layers are almost vertical and end downwards in the usual position. Lacunæ (*lac*) have appeared opposite the up-turned wing of the host's cortex, and the inward projection from the collapsed layers is much lower down than in *Santalum album* (*Sant. II*, Plates XIII, XIV, etc.).

The nuclear cells are practically devoid of contents and show signs of breaking up irregularly (*a*). The sucker is distinctly lobed and it is to be noted that it is provided with secreting cells on its sides as well as at its end, the whole inner sides of the wings being coated with yellow secretion. A cap of clear yellow substance is to be found at the end of each wing (*x*) (see para. 10 and Plate VII, fig. 4, for the mode of formation of this cap).

It was stated in a recent paper (*Par. Trees*) that compound haustoria were to be met with among those of *Cansjera Rheedii*. This does not appear to be the case, and the section on which the remark was based appears, on closer examination, to be abnormal. This is one of the few characters of these haustoria in which they resemble those of *Olax* rather than *Santalum*.

In the median line, where the sucker meets the wood of the host, the traces of a former gland may be made out (*gl*).

The development of the haustorium of *Cansjera Rheedii* has thus been followed from an early stage to the mature organ, and the points of difference noted between it and the similar organs of *Olax* and *Santalum*. It will now be necessary to consider certain tissues in greater detail. In this study the arrangement followed in *Olax* will best serve our purpose. The haustorium as a whole and the various tissues of the cortex and nucleus will be first examined, after which the vascular system and the sucker will be separately dealt with. Lastly, the effects produced upon the various roots attacked and their

tissues will be noted and a summary statement prepared of the characteristic features of the haustoria as contrasted with those of *Santalum* and *Olax*.

Tissues of the Mature Haustorium.

9. *Cork and Lenticels.*—Cork is very common in *Cansjera* haustoria, much more so than in *Santalum*, but its presence does not discolour the surface of the root as it does in that plant. The cork in *Cansjera* is whitish yellow, and this is the prevailing colour of both its young and old haustoria. It will be remembered that in *Santalum* the cork forms a bright red-brown layer and that the older roots as well as the haustoria assume this colour.

In *Cansjera Rheedii*, cork is frequently continued round the cortical folds as far as the top of the wings of the host's bark. In one haustorium fixed on a root of *Cansjera* itself very thick layers have been formed both by the host and parasite. In the sections of this haustorium the cork is seen by transmitted light to be of a dark colour, while the phellogen is seen on each side as a thin white band (Plate XI, fig. 3).

Lenticels are common in *Cansjera* haustoria, and it is doubtless due to them that the haustoria have so irregular and warty a surface (Plate IX, fig. 1, *lent.*).

Hypoderm.—This, as has been noted, is usually to be found in *Cansjera* haustoria, although it is more distinct in some than in others. It consists of a layer of parenchymatous cells, within the cork, whose contents are peculiar. Starch grains are not found in any great abundance and, when formed, are hidden by the granular contents. The latter persist even in old specimens and are distinguished by their tendency to assume the form of drops. The hypodermal layer is distinguishable by means of this feature after all the rest of the tissues are emptied of their contents. The shape and size of the cells are also different from those within, for, while the latter become extended with the increase in size of the haustorium,

the cells of the hypoderm remain small and equal-sided to the end. The structure and appearance of the hypoderm may be studied in Plates II, III, V and, especially, Plate VI, fig. 1, and Plate VII, fig. 5.

The Collapsed Layers.—These are simple in structure and are formed as in *Santalum*. They extend upwards, when fully developed, to just outside the point where the endodermis ceases (Plate V, figs. 1 and 2, and Plate VII, fig. 1), thus differing totally from those in *Olax*. In very old haustoria, however, they are left far behind by the secondary thickening of the xylem and form an insignificant part of the haustorium (Plate IX, fig. 5). Their usual downward ending is, as stated, peculiar. Instead of passing to near the ends of the cortical folds as in *Santalum*, they end half-way between this point and the edge of the host's wings. It is possible that this position may be partly the result of the secondary thickening which so frequently takes place in the end of the fold, but, whatever its cause may be, the result is that the collapsed layers soon become vertical (Plate V, fig. 2), and, as secondary thickening proceeds, ultimately converge downwards (Plate IX, figs. 1 and 2). A few cases have been met with in which the cortical folds remain long and thin, having no secondary thickening. These extend further round the attacked root than usual, and their collapsed layers also pass towards the ends of the folds.

The lacunar region inside the collapsed layers is situated much lower down than in *Santalum* and *Olax*. The tissue within the upper parts of the collapsed layers is free from breaks, but, outside the cortical wings of the host, the cells are crushed and separated by a series of characteristic lacunæ (Plates V and VI).

The collapsed layers first appear in the cortex between the starch-laden cells and the larger, empty cells without. They are formed, as in *Olax* and *Santalum*, from the decay of masses of crushed cells in the cortex. In *Cansjera* all the additions appear to be from the inner sides. The cortical cells on the outer side thus usually retain their form and are not

crushed, while those within are obviously compressed and show undulations on their radial walls. The outer part of the collapsed layer is usually the oldest and, in late stages, becomes yellow and homogeneous, while the inner parts are still white and show their manner of origin from flattened cells. This decay of the outer part of the collapsed layers is not infrequent, and the application of staining reagents shows that a change in substance is taking place and that the outer parts are always more altered than the inner.

In conclusion, the small part played by the collapsed layers and the cortex generally in old haustoria reminds somewhat of what takes place in *Buckleya Quadriala* according to Kusano.* Here cork continues to be formed at increasing depths in the cortex, until ultimately almost the whole of cortex including the collapsed layers is thrown off.

10. *Yellowing of the tissues.*—Masses of yellow, transparent substance are not uncommon in the haustoria of *Cansjera Rheedii*. These are found not only in the vascular system, as in the interrupted zone and the older secondary wood, but in many parts of the nucleus and cortex, which habitually undergo disintegration.

In young haustoria which for some reason have been arrested in their growth, large lacunæ are not infrequent (Plate III, fig. 3). These are lined with yellow, transparent substance, formed by the breaking down of the cells whose places the lacunæ occupy.

In cases where the cortical folds have failed to grasp the object attacked and are thus brought into contact with the sides of the sucker, the space between these parts is filled with a similar yellow substance. This is also not uncommon in *Santalum* (*Sant. I*, figs. 14 and 15, *gl*). The lumen of the gland, again, after it has ceased its activity, is usually filled with yellow substance.

* Kusano, S., Studies in the Parasitism of *Buklеya Quadriala* B. et H., a Santalaceous Parasite, etc. Journ. Coll. Sc. Imp. Univ. Tokyo, XVII, No. 10, 1902.

In older haustoria of *Santalum* the cells along the top of the nucleus become crushed and form a well-marked collapsed layer (*Sant. II*, Plate XI, fig. 2), and this is sometimes the case in *Cansjera*. But in the latter case the transverse band of cells more frequently becomes separated irregularly and disintegrated to a clear, yellowish brown mass (Plate IX, fig. 1, *b*).

More interesting is the presence in many sections of a small cap of brilliant yellow substance of the end of the host's disrupted cortex, and it is in most cases quite easy to see that this cap is made up of crushed haustorial cells (Plates V, fig. 2, *x*, and VII, fig. 4). In *Olax* and *Santalum* crushed masses of tissue are usual at this place, but they remain as such and are not fused into a yellow mass.

With these cases in view, it is not surprising that the collapsed layers themselves are sometimes converted into yellow bands, and haustoria have been noted in which a clear transition can be traced from the white walls of freshly added cells on the inner side of the yellow fused mass of older tissue outside. On Plate VI (fig. 6) a haustorium is drawn in which the collapsed layer has undergone complete disorganisation. The cell walls of which it was composed have become a clear yellow band. This yellow band is continuous downwards along the inward projection to the yellow cap at the end of the host's wing, and this last may be traced, through the clear, yellow substance which lines the inner side of the host's wing, to the yellow mass which is always found opposite the end of the sucker lobes. We have thus an instructive continuity between the yellowing of decaying haustorial tissues and the film of yellow "secretion" which spreads over the host's tissues wherever they are in contact with the sucker cells. This substance is again referred to in paragraph 18, where an attempt is made to trace its origin.

11. *Internal Meristems.*—The yellowing of the tissues described in the last paragraph is not infrequently accompanied by activity in the neighbouring cells which had, to all

appearance, already become permanent. A series of parallel walls are formed and a layer of cells resembling cork makes its appearance, surrounding the decayed part. Thus, in the case of the yellowed collapsed layers figured on Plate VI, the cells on both sides have developed in a meristem-like manner. Similar secondary tissue has been noted around the lacunæ in young haustoria and the yellow band of decayed cells across the upper part of the nucleus.

It is natural to assume that this cell-formation has for its object the provision of a separating layer of cork by which the dead tissues may be cut off from the living. It is to be noted in passing, that the cells thus formed are sufficiently turgid to project into the yellow mass, much as the external cells of the sucker project as papillæ into the mass of yellow secretion. It is probable that in both cases the form assumed is due to purely mechanical conditions.

The cortical cells on the outer sides of the collapsed layers soon lose their contents and become apparently moribund. There is none of the radial arrangement of the cells which forms so marked a character of the old haustoria of *Olax scandens*, and the cells of this part are similar to those of *Santalum album*. And this similarity is emphasised by the occasional appearance in this place of meristematic cells resembling those found in haustoria of *Santalum album* attacking the roots of *Pithecolobium dulce* (*Sant. II*, Plate V, fig. 1, *me*).

A much more striking feature is the occurrence of secondary thickening in the ends of the cortical folds, mentioned in para. 7 (Plate V, fig. 1). This appears to be independent of the lignification of a small patch of cells in the end of the cortical fold noted in para. 6 (Plate IV, *j*). There is a tendency in certain plants for this lignification to extend upwards as a narrow band, three or four cells broad, immediately below the hypoderm (Plates VI, fig. 7, and VII, fig. 5). It is thus not infrequent for the outer layers of the haustorium to assume some complexity, and this has been noted especially in the case of certain hosts. For instance, while no trace of the

lignified cells appears in the folds of haustoria clasping the roots of *Commelina fruticosa*, it is present in most if not all of the dozen or so examined which were attached to *Hemidesmus indicus* and *Capparis horrida*.

12. *Crystals of Calcium Carbonate.*—As has been pointed out by Edelhoff* and Valeton† there are no calcium oxalate crystals in the tissues of *Cansjera*, their place being taken by crystalline cystoliths of calcium carbonate. Masses of calcium carbonate crystals, although rare in young haustoria, are abundant in older ones, being presumably only formed in cells whose activity is on the wane. Thus, certain tracts of cells which are no longer required by the haustorium are noted for their frequent appearance. The crystals occur in the elongating portion of the inner cortex, inside the collapsed layers near the lacunar tissue, in the cortex outside the collapsed layers and, especially, in the ground tissue immediately above the nucleus (Plates VI, IX and XI). They are rarer in the hypoderm and are not formed in the nuclear tissues. The distribution of these crystal masses is thus mainly cortical, and follows with remarkable fidelity that of the calcium oxalate crystals in the haustoria of *Olax scandens* (*Olax*, para. 16). The presence of these bodies has been noted in some forty haustoria, but was probably more widely spread in the original material because many of the sections were mounted in dilute glycerine and lay for some time before examination. In some sections, at least, the crystals have been noted gradually to disappear in this medium. In these cases no definite structure was left behind and no residual basis has been found giving callose reactions (see Plate VI, fig. 2, *x*, and the description of this figure). Fresh material has not been available for the examination of these bodies, but, from the spirit material at

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* Edelhoff, E., Vergl. Anat. des Blattes der Familie der *Olacineen*. Engler, Botan. Jahrb. VIII, 1886-7.

† Valeton, Crit. Overz. d. *Olacineen*, Groeningen, 1886. (I have not been able to see this paper.)

command, they do not appear to resemble the double cystoliths described for *Cansjera* by van Tieghem.*

They occur in isolated cells and the manner of deposition appears to be rather that of ordinary calcium oxalate crystals than of normal cystoliths. They form masses of clearly defined tabular crystals of calcium carbonate *or* a mulberry-like mass with blunt and frequently branching projections (Plate VI, figs. 2 and 3). In one case a quite different form is assumed. In the outer cortex of some sections the crystals of calcium carbonate have taken on the appearance of sphærocrystals (Plate VI, fig. 4). Such crystal masses, instead of belonging to one cell, project into two or three from their common angle. At the place of junction a substance is found which stains deeply with methylene blue. In the haustoria where these occur, the radiating crystals were found in the outer cortex, while the crystal masses in the inner cortex had the normal form described above.†

In a few cases the walls of the cells in which the crystal masses occur have become sclerotic (Plate VI, fig. 5). These thick-walled cells call to mind the sclerotic cystoliths found in Champereia.‡

Isolated thick-walled cells are found scattered throughout the cortex of *Cansjera* haustoria. Their usual position is

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* Van Tieghem, Recherches sur la Structure et les Affinités des *Thymeleacées* et des *Pencacées*. Ann. d. Sc. Nat. Ser. VII, Bot., T. XVII, 1893 : pp. 249-257, *Cansjera*, *Champereia* et la Famille des *Opiliacées*.

† The facts concerning these supposed radiating crystals of calcium carbonate are as follows. They were found in sections of several haustoria attacking *Capparis horrida* roots. In these haustoria the ordinary crystal masses were present in abundance in the usual places and the radiating crystals were confined to the ends of the cortical folds. Upon the addition of dilute acetic acid all the crystals disappeared rapidly, with the evolution of bubbles of gas, but it was not possible to assert that any of this gas came from the masses of radiating crystals, because it made its appearance at points of the sections far removed from any crystals.

The radiating crystals do not exhibit the true structure of sphærocrystals as described by Hansen. They are simply groups of crystals projecting into several cells from a basis of amorphous substance which was readily stained. There was no outer shell or skin visible. It is possible that they do not occur in fresh material, but have been slowly formed, like sphærocrystals, in the alcoholic material. (See Ad. Hansen, Ueber Sphærocrystalle, Arb. Bot. Inst. Würzburg, III, 1888.)

‡ Solereder, Syst. Anat. d. Dicotyledonen, 1899.

outside the collapsed layers (Plate VI, figs. 1 and 5), but they are sometimes found along with crystals of calcium carbonate in the elongating cells of the inner cortex In a few cases, as stated above, the crystals are found inside them.

The Vascular System.

13. The *general arrangement of the vascular system* in the haustorium of *Cansjera Rheedii* is similar to that described already for *Santalum* and *Olax*. A branch from the vascular cylinder of the mother root spreads out to form a widening circle of bundles in the transitional region. At a certain point these bundles are broken up, and isolated rows of vessels, separated by parenchyma, are uniformly distributed over a broad circle round the central mass of ground tissue. This has been regarded as the region where the mother root joins the haustorium proper. Below it, the vessels are seen to branch repeatedly so that their number increases greatly. They are, moreover, no longer separated, but fuse to a dense mass of xylem arranged in a broad oval ring. This ring rapidly flattens downwards, at the same time becoming discontinuous at two opposite points, so that, ultimately, two parallel lamellæ are formed which pass down the axis of the haustorium. This is the arrangement in *Santalum*: it will be remembered that in *Olax* only one plate of vessels is found in the axis of the haustorium. Lastly, the bundles become broken up again and the vessels form separate rows in the sucker as it approaches the host's root. A closer study of this general arrangement need not detain us longer, as it has been fully dealt with in previous papers (*Sant. II*, Plates IV and VI—VIII)

Certain parts of the vascular system are, however, peculiar in *Cansjera* haustoria. The endodermis, occasionally noted in *Santalum*, but of so problematical a nature in *Olax*, is very clearly defined. The interrupted zone described in *Santalum*, but totally absent in *Olax*, has its greatest development in *Cansjera*. As in *Santalum*, no bast is found in the

haustorium, even in cases of self-attack: in *Olax*, it will be remembered, the presence of masses of sieve-tubes and other bast elements was a surprising but well-marked feature in cases of self-attachment. In older haustoria with much secondary thickening, a mass of cambiform tissue filled with contents is found outside the cambium, forming, as in *Santalum*, a sort of secondary cortex. Secondary thickening is practically confined to the upper part of the vascular loop, and this fact gives a peculiar and characteristic appearance to sections of old haustoria. Lastly, there is a marked difference in the size and pitting of the vessels of the sucker and those of the mother root. These points of interest will be dealt with in order.

14. The *Endodermis* is extremely clearly shown in the upper part of the haustorium of *Cansjera Rheedii*. It is, however, confined to the mother root and transitional region and stops short at the interrupted zone (Plates V, fig. 2, and VII, fig. 1). In ordinary haustoria it is seen to consist of a layer of crushed cells whose walls are much darker in transmitted light than those of the cells around them. Here and there, in sections of young parts, there are shadows on the walls, and in rare cases this is seen to be due to undulations similar to those in the endodermis of many roots. An endodermal layer appears to surround each bundle where they are separated in the transitional region, but good figures of this are not easy to obtain.

The *Interrupted Zone* is very well developed in these haustoria. The change undergone by the vessels of this region is exactly that described for *Santalum album* (*Sant. II*, para. 9). The walls lose their characteristic markings and assume a yellow colour and, in later stages, the whole vessel becomes filled with yellow substance, the lumen being entirely obliterated. The interrupted zone occurs at the point of junction of the transitional region and the haustorium proper, just above the place of greatest width of the vascular loop and in the place (mentioned above) where the bundles of the transitional

region separate to isolated rows (*Sant. II*, Plate VI, fig. 2, *a*, *a*). They are here separated by thin-walled, small-coated parenchyma (Plate VII). A curious circumstance about this interrupted zone is its extremely early appearance, some of the first stages of vascular development met with showing complete disorganisation at this point and, presumably, a complete dislocation of the vascular system. In other cases, however, it has been observed that the outermost strands are still normal while the inner ones are yellowed. The yellowing is centrifugal, and passes outwards in much the same manner as the duramen in the secondary wood, only it is much more rapidly completed. In the figures on Plate VII these points are illustrated. In the first two figures yellowing is complete, mere traces of pitting alone being found on the outermost row of vessels. In figure 3, however, the outer row is apparently still intact, while all the rest are filled with gummy substance. It should be noted that the last mentioned case is not very common and the appearance shown in figures 1 and 2 is more usual.

As already remarked (*Sant. II*, para. 9), it is difficult to understand the utility of this arrangement, for it would appear that interruption occurs very shortly after the sucker has reached the woody cylinder of the host and soon after the fusion of the vascular systems of the two plants. The conclusion at present arrived at is that the activity of the haustorium is extremely short and that, as in ordinary plants, the absorbing portion of the root-system in these parasites functions only for a short time, and this absorbing power is passed onwards as the roots grow in length, branch and encounter new foreign systems to which to attach themselves. According to this view, the parasite is brought into contact with new roots in rapid succession and the old suckers are practically closed. If this be true, on the other hand, it is difficult to understand the amount of secondary thickening which takes place in some haustoria, the new vessels being apparently closed in succession almost as fast as they are formed (Plate IX, fig. 5).

To learn what really happens in these organs will, however, have to be left until they can be studied in the field. We shall there perhaps be able to test whether there is any passage of fluids in the older haustoria and, if so, by what path they pass upwards. Such experiments have not been possible up to the present.

Before leaving the interrupted zone, it may be remarked that the rows of vessels in this region are fairly equidistant. The number of strands varies according to the amount of secondary thickening which has taken place, and, in general, a fair idea may be obtained of the age of a haustorium by counting the number of strands present. In very early cases a single strand is seen, while, in old, distorted haustoria, it is not infrequent to count as many as 40 in the section on each side (Plate IX, fig 5).

15. The *Cambium* is distinctly seen in all parts of the vascular system, although it is less marked towards the sucker than in *Olax* and *Santalum*. Its activity and length of life, however, seem to vary in different parts of the haustorium and, in this respect, *Cansjera* differs from both the haustoria already described. Speaking generally, the cambium is short-lived in the axial region and it probably very soon ceases to produce wood there, while, passing upwards, its activity increases, until, in the middle of the vascular loop, a great development takes place. This will be rendered clearer on reading the paragraph on secondary thickening.

The *vessels* are uniform in character in the haustorium proper, long and narrow, richly perforated with wide, irregular pits which frequently extend right across the width of the vessel (Plate VIII, figs. 1, 2 and 5). In this latter character they differ remarkably from the vessels of the transitional region and mother root. Here the pits are small and oval and are arranged in regular lines over the surface of the wide vessel (fig. 4). Just as in *Olax*, while the vessels of the sucker present one extreme and those of the mother root another,

numerous transitional cases occur in the body of the haustorium (*Olax*, 28 & 29). The vessels of the mother root are, as might be expected, much wider than those of the haustorium proper.

In one place the vessels are peculiar, and it is doubtful if they have much to do with the transmission of fluids. This is at the top of the axis, where the two bands of vessels separate outwards to curve round the loop. On the inner edge of the vascular loop at this point the vessels are broad and short, have in fact much the shape and size of the neighbouring cells of the nuclear "pith" (Plate VIII, figs. 2 and 3, *sq.*).

Bast has not been met with in the haustorium proper of *Cansjera*. The sieve-tubes of the mother root are very small and difficult to locate, and little callus-formation has been met with in the sections, although the haustoria were collected at different times of the year. As far as can be seen, the sieve-tubes are found as far down as the end of the endodermis (Plate VII, fig. 2), but no trace of them has been met with lower down, even in cases of self-attachment. It will be remembered that, in *Olax scandens*, an abundant development of bast occurred throughout the haustorium in the latter case.

In certain sections, especially in old haustoria (Plate IX, figs. 1 and 5, and Plate XI, fig. 3), a well-defined mass of tissue in regular layers is found outside the cambium. It is possible that a store of material is here laid up for the formation of further vessels in secondary thickening. On the other hand, it is just here that fewest vessels are formed. The tissue has much the appearance of secondary cortex, the latter being usually crushed and dead in old haustoria, especially in the lower parts. A protection would thus be afforded to the cambial cells within.

16. *Secondary thickening* of the vascular system differs considerably in *Cansjera* haustoria from that in *Olax* and *Santalum*. In the latter (*Sant. II*, Plate IX), wood is developed equally throughout the haustorium, as much in the sucker and axis as in the vascular loop. In *Olax*, however (*Olax*, Plate

IX, figs. 6—10), we see that the increase in thickness of the vascular strands assumes its maximum in the lower part of the vascular loop. In *Cansjera* this tendency is increased to such an extent that comparatively little thickening takes place in the sucker or axis, and the addition of secondary wood is chiefly in the middle of the vascular loop, immediately below the interrupted zone. This feature gives the old haustoria a very characteristic appearance. In them there is a curious bell-shaped expansion of the wood on each side of the loop, terminating upwards in the isolated strands of the interrupted zone. The haustorium thus becomes broader at the top with increasing age and the collapsed layers assume a vertical position (Plate IX, fig. 1). In very old haustoria the effect is still more striking. The whole haustorium assumes a turbinate form, the upper part being very broad and the point of attachment frequently minute (Plate I, figs. 5 and 6), like the peg of a top. The collapsed layers in such haustoria are inconspicuous and ultimately become almost horizontal, the cambiform tissue is broad and the cortex is reduced to a narrow strip charged with calcium carbonate crystals (Plate IX, fig. 5).

Yellowing of the old wood is not a very marked character in *Cansjera* haustoria, but it is met with here and there. It is interesting to note that, in this matter, as in so many others, *Cansjera* resembles *Santalum* rather than *Olax*. In the latter the yellowing commences in the primary xylem and gradually extends outwards through the secondary wood. In *Santalum* and *Cansjera*, while the inner layers of secondary wood become yellowed with age, the primary xylem remains white in colour like the younger part of the secondary wood.

The Sucker.

17. *Penetration.*—It is assumed that the chief reason for the penetration, by green hemi-parasites, of the roots of other plants is to form a connection through the haustorium between the vascular systems of the host and parasite. By

this means the stream of water and salts will be tapped and the deficiency in root-hairs will be rectified. Let us consider the difficulties in the way of such penetration. Roots are protected externally by a bark largely composed of cork. Added to this, there are frequently thick-walled cells in the cortex, which vary from isolated bundles to uninterrupted bands of considerable thickness. The rest of the cortex consists of parenchyma, frequently starch-laden, and there may or may not be a sheath of sclerotic cells around the central vascular cylinder. On the whole, the roots of monocotyledons, and especially palms, appear to be better provided with such protective layers than those of dicotyledons, a fact that may be connected with the looser structure of their vascular cylinder.

The first obstacle to be overcome is the cork. It is improbable that the ferment secreted by the haustorium has any great power of dissolving cuticularised membranes, cork indeed being, usually, a successful protection of the invaded tissues of the host from further attack, and some other way of removing the cork is needed. In paragraph 3 of this paper it was suggested that the firm adhesion of the young haustorium to a host's root may be due to the secretion of a gummy substance. As the haustorium increases in width, a shearing action is thus brought into play, causing the layers of cork to be rolled apart (Plate I, figs. 8 and *b*). Compare this with *Sant. II*, Plate V, figs. 2 and 2′). In other cases strands of cork are lifted bodily away, as shown in *Sant. I*, figs. 15, 16 and 18. This action of the superficial layers of the haustorium together with the undoubted pressure exerted, is probably sufficient to account for the successful penetration of the bark, even when composed of thick layers of corky tissue.

The sclerotic bands appear to be more difficult to negotiate, especially when they are lignified. We have seen that, when they are discontinuous, the sucker, passing along the line of least resistance, avoids them and finds its way through the parenchymatous tissue between (Plate X, fig. 4, and *Sant. II*,

Plate XI, fig. 2). But where the bands are at all continuous, great difficulty is experienced. This is shown in *Santalum* by the formation of compound haustoria and, in some cases, such as *Zizyphus* and various monocotyledons, the haustorium is frequently defeated in its attempts at penetration. The same applies to continuous sclerotic sheaths round the vascular cylinder. Progress is very slow and the haustorium is often found to be shrunken and moribund before entrance has been effected (*Sant. I*, Plate VI, fig. 29).

In an ordinary attack on a dicotyledon root we may thus assume that the cork is lifted piece-meal, while the sclerenchymatous bands are either very slowly dissolved or, more frequently, avoided altogether. The main work left for the secreting cells is the dissolution of the cortex and bast, and this is done with great rapidity and success by the ferments in the haustorium. It has been pointed out that, in *Cansjera*, as in *Santalum*, the presence of a gland is not necessary for penetration, this work being accomplished by secretions from the ordinary surface cells, probably aided by the cells of the nucleus.

The mode of penetration varies in character in *Cansjera*, as in the other haustoria examined, according to the hardness of the root attacked and the distribution of its thick-walled protective cells. In soft roots, with loose or lightly lignified woody cylinder, the latter is penetrated by the sucker, either all over or down the medullary rays. Occasionally the sucker wanders between the sclerenchymatous bands in the cortex, but, on the whole, these irregularities are much less frequently met with than in *Santalum* and *Olax*.

18. *The Sucker.*—This part of the haustorium, as we have seen, is formed chiefly of nuclear cells in *Cansjera Rheedii*, and the cause of its rapid entry is to be put down to the great accumulation of such cells inside the young haustorium and their sudden expansion the moment a split is formed in the bark. Some of the inner cortex, distinguished by the absence of starch

in its cells, also takes part in the formation of the sucker (Plates IV and V). As in *Santalum*, the sucker of *Cansjera* consists partly of nuclear and partly of cortical cells: that of *Olax* is purely nuclear.

The further development of the sucker in *Cansjera* is extremely limited as compared with that in *Santalum* and *Olax*. Having reached the woody cylinder, and being prevented from further progress in this direction, it spreads along the cambial line and thus becomes bilobed. But the lobing in *Cansjera* is very slight and sometimes altogether absent. In not a few cases the sucker remains plug-like or columnar (Plate IX, figs. 1 and 5). This is in marked contrast with the long-continued growth of the sucker lobes in the other haustoria. Besides this, the sucker does not greatly increase in thickness, and, as a consequence, the wings of host's bark thrust aside by its entry are comparatively small. It may be noted, in passing, that the haustoria of *Ximenia americana*, although not yet fully examined, appear to present the opposite extreme, as well in the growth of the sucker lobes as in that of the cortical folds. Both of these grow right round the opposing root until they completely envelope it. One result of the meagre development of the sucker in *Cansjera* is that the whole haustorium, from the start almost, is much broader above than below, a character which becomes intensified when secondary thickening takes place in the vascular system.

On the other hand, the sucker is not active only at its end where it touches the woody cylinder of the host's root, but also at its sides where it is in contact with the cortex and bark. A thick layer of yellow substance lines the inner sides of each wing, and the cells of the sucker extend as papillæ into this layer just as they do at the edges of the lobes. At some later period the active cells at the sides are usually cut off from the main body of the sucker by a collapsed layer, and when this happens, they rapidly become permanent and are ultimately crushed (Plates X, figs. 1 & 2, *a*, and XI, fig. 1). A similar state of things has been occasionally met with in *Santalum*.

The vessels in the axis and the sucker behave much as in *Santalum* and *Olax*, with the exception already noted that there is comparatively little secondary thickening. As the host's tissue is approached, they form separate rows and apply themselves to different parts of the woody tissue. As in the other haustoria, there is no special tendency for these rows to apply themselves to the vessels of the host and, in most cases, no definite connection can be noted between the vessels of host and parasite. Occasionally, however, we find vessels formed in the sucker accurately opposite to the vessels of the host. Two such cases are figured on Plate X (figs. 1 and 4) and call to mind a similar example mentioned in our study of *Santalum* (*Sant. II*, 29).

A few lines, in conclusion, may be devoted to the yellow "secretion" so often referred to as occurring between the sucker and the host's tissues, for some additional light has been thrown on its origin and structure by the examination of *Cansjera* sections (Compare Plate X, fig. 2, with *Sant. II*, page 31, and Plate X, figs. 1—3, and *Olax*, Plate X, fig. 2). In the purely glandular cells and the lumen of the gland the yellow transparent substance is obviously the direct product of the protoplasm accumulating beneath the cuticle and being discharged at intervals. A yellowish colour is not infrequently assumed by discharges of this kind (Marshall Ward, for instance, noted this colour in the secretion from *Botrytis* hyphæ on *Lilium candidum*). In the more diffused action of the general haustorial surface, the yellow substance has not infrequently traces of structure, many instances of striation or lamination having been noted. This lamination appears to be caused by the breaking down of successive cells (refer also to paragraph 10 where the yellow substance formed by the breaking down of the cells of the collapsed layer are clearly continuous with the yellow secretion at the end of the sucker). In some cases these cells belong to the sucker, and it is natural to suppose that they have been dissolved by the action of the cells behind them. In other cases the yellow layer is evidently formed in part

by the crushed cells of the host. The whole mass is probably filled with ferment formed in the haustorial cells, and, while the remains of haustorial cells are added on the one side, those of the host may sometimes also be seen on the other, and the mass thus assumes a considerable thickness (Plate X, fig. 2, *b*). Long after the secreting cells have lost their activity, it would thus be possible for the yellow mass to continue its action on the host's tissues, until the latter are effectively protected by the formation of a layer of cork. Sooner or later various pigments are added to the mass and it assumes colours characteristic of different hosts. All stages from clear yellow (*Citrus*), through reds and browns (*Acacias and Albizzias*) are met with, until, in such plants as *Diospyros* and *Strychnos*, the colour becomes an inky black.

It is interesting to note that this coloured separating substance is always wanting opposite to the rows of vessels in the sucker (Plate X, figs. 1 and 4), a fact tending to show that absorption no longer takes place where the yellow substance is formed. A study of fig. 2 on Plate XI leads to the same conclusion. In staining for starch, the tissues of host and haustorium were coloured blue wherever the dark secretion layer separated them (*st*). In other places no coloration was observed. It is obvious that no active flow of nutriment takes place where the cells are full of starch.

Effect on the Host's Tissues.

19. The general effect of the haustorial action on the host's tissues is similar in *Cansjera* to that in *Santalum* and *Olax*, but the sucker is smaller, and this seems to cause certain differences.

The wings of the host's bark are uniformly attacked, as we have seen, by the active sides of the sucker. The attacked parts are generally cut off by a layer of cork from the living cells of the host's root. The wings are, however, small, probably on account of the poor development of the sucker. And this

poor development will also probably account for the fact that the secondary growths, which form so marked a feature in the attacks of *Olax scandens*, are almost entirely absent in the roots entered by *Cansjera*. Secondary growth of any kind (excepting of course the formation of corky separating layers) is very rare in the wings of the cortex, and the formation of secondary wood there is practically unknown.

The formation of cork in the angle opposite the edge of the sucker lobe is frequently met with, and this is usually sufficient to bar further progress. The origin of this cork is well seen in one section through the root of *Plumbago rosea*. The phellogen appears to arise from a row of cells derived from the cambium. Instead of becoming lignified in the usual way, these cells divide by radial walls and thus form tangential rows of cork. In certain cases noted, this corky protection of the cambium is neglected or insufficient, the action of the sucker cells extending far beyond the place occupied by them. Thus, in a couple of haustoria fixed on *Alangium Lamarckii*, the destruction of the cambium passes nearly all round the root, although the lobing of the sucker is, as usual, small.

Secondary thickening of the woody cylinder of the host, after attack, occurs in a few cases, but it is rare. Is this because of the smallness of the haustorium or its comparatively short duration? Or is it due to the fact that these haustoria have been collected in a dry region where growth of any kind is slow?

Some of the roots attacked have abnormal structure. Considering the differences noted in the structure of haustoria attacking monocotyledon and dicotyledon roots (*Sant. I*, 14), it is interesting to mark their behaviour in these cases. In *Ærua lanata* the wood occurs in concentric, more or less continuous bands, and these are mainly composed of thick-walled elements. Where these bands extend right across the area of contact, the sucker treats them as ordinary woody cylinder and spreads along the cambium. If there is any gap, however, the sucker passes through it and attacks the band within, the

outer layer of wood with its layer of cambium being treated exactly as if it were a sclerotic band (Plate X, fig. 4). The scattered bast bundles in the wood of the root of *Strychnos Nux-Vomica* do not appear to materially affect the course of the sucker.

The vessels opposite to the sucker are, for the most part, filled with gummy substance of varying colour. In a few cases a dense black pigment is present.—*Azima tetracantha, Mallotus distans, Strychnos Nux-Vomica, Barleria buxifolia.* Thyloses occur in the vessels of certain species and are of special interest in two cases. In *Vernonia travancorica* and *Argyreia speciosa* they become thick-walled and pitted (Plate IX, figs. 3 and 4), a single thylose sometimes filling up a vessel so as to present the appearance of one vessel inside another. In *Vernonia travancorica,* some of the thyloses are filled with crystals of calcium oxalate (fig. 2).

20. *Action of the Secretion on Starch.*—This has already been referred to (*Sant. II,* 33 and *Olax,* para. 17), and it was demonstrated from a study of many sections that the ferment was more active in the destruction of cellulose cell walls than of their starchy contents. The study of the sections of *Cansjera Rheedii* haustoria leads to the same conclusion, and the following remarks may be added to those already made.

In the rapid progress of the sucker through the cortex the starch grains are of minor importance, the object being presumably to penetrate the tissues as soon as possible by the solution of the cell-walls. Starch grains are thus not infrequently found in the yellow mass of substance formed by the outpouring of secretion from the glandular cells and the breaking down of the cell-walls. But this is not all. In not a few cases there appears to be a definite accumulation of starch in this layer when no such substance is to be found in the neighbouring cells. In other cases, there is a dense mass of starch in the woody cylinder exactly opposite the sucker end, while there is none in the rest of the root attacked. This is the case

in several sections cut through the roots of *Capparis zeylanica* and *horrida*. Further, in the wings of the host's bark cut off by cork, the cells of which are browned and evidently decomposed, it is not uncommon to find masses of starch grains while the rest of the cortex is almost quite clear of contents (Plate XI, figs. 1 and 1*a*). How are we to explain the presence of such quantities of stored carbohydrate in these places ?

It might be suggested that, while the transverse connection of parts in the attacked roots has been interrupted, a passage of substances might take place lengthwise. But longitudinal sections show that the dead cells of the wing are cut off in this direction by cork as well as across the section. It is, again, possible that the cortical cells were cut off at a time when all the tissues were charged with starch which has been subsequently translocated in the free tissues, but blocked by the cork in those cut off, or, indeed, that this very formation of cork or the formation of thyloses and gum in the vessels has taken up the superfluous starch. But a careful study of the sections does not incline one to this view, and this explanation could hardly be offered for the accumulation of starch in the yellow substance.

It looks very much as if, in these cases, the last act of the protoplasm, before or after the destruction of the cell-wall, was the deposition of starch from the excess of carbohydrates available from the action of the ferment in dissolving the cell-walls. We learn from Peirce's observations on *Cuscuta glomerata* attacking balsam leaves,* that the ferments act first on the cell-wall and last on the protoplasm, and that the mesophyll cells are capable of forming fresh starch for a considerable period after they have been attacked by the sucker cells. It may be noted in passing that this accumulation of starch is only characteristic of attacks on certain plants. Thus in *Morinda tinctoria*, penetrated by *Olax* haustoria, it is almost invariably

* Peirce, G. J., On the Structure of some Phanerogamic Parasites, Annals of Botany, Vol. VII, 1893.

present in the yellow layer at the sides and ends of the wings. In *Capparis horrida* and *Azima tetracantha*, on the other hand, the wings themselves are almost always gorged with starch grains, even when they are old, browned and collapsed, while the neighbouring tissues are empty (Plate XI, figs. 1 and 1*a*).

If the explanation offered, namely, that the formation of starch in these places is due to the last act of the moribund protoplasm, is insufficient, one is tempted to refer to the reverse action of ferments demonstrated by Cross Hill in concentrated solutions of glucose.* The building up of starch by such reverse action has not been observed at present, but the presence of these masses of starch in the sections is very striking and, until a more satisfactory explanation can be arrived at, this suggestion may be recorded.

The physical effect of the secretion on the starch in the host's tissues appears to be that it swells up considerably and ultimately disappears (*Olax*, Plate VIII, figs. 4 and 5, and *Sant. II*, Plate II, fig. 2). It is interesting to note that starch in the haustorial cells is acted on in a different manner when about to be translocated, the grains in this case becoming minutely subdivided and suffering fragmentation (Plate XI, fig. 1*a*, *x*, and *Olax*, Plate VIII, fig. 3).

Comparison of the Haustoria of Cansjera, Olax and Santalum.

21. It may be useful to conclude our study of the structure of the haustorium of *Cansjera* with a summary of the points of difference between it and the haustoria already familiar to us, those of *Olax* and *Santalum*. As might be expected from the remarks in paragraph 1, *Cansjera* haustoria are very similar to those of *Santalum*: in fact, to determine the points of difference has necessitated a much more detailed study than was at first contemplated. Many of these points are of

* Cross Hill's work on reverse action of maltase in excess of glucose is referred to in Green, J. R., Fermentation, 1899, p. 436.

very minor importance, as will be seen directly. The differences from *Olax* haustoria, on the other hand, are so many and great that their mere enumeration would mean a recapitulation of much of this and the preceding paper in this series. In only three particulars has the haustorium of *Cansjera* been found to resemble that of *Olax* rather than that of *Santalum:* the haustorium is whitish and not coloured brown with age, no compound haustoria have been met with and secondary thickening in the wood is greater in the vascular loop than in the axis. In the characters now to be mentioned the haustoria of *Cansjera* differ as much from *Olax* as they do from *Santalum.*

The haustorium of *Cansjera* is smaller and less regular than that of *Santalum,* the early irregularities being apparently due to the abundance of lenticels which are not found in *Santalum.* In extreme age the haustorium frequently becomes fantastically lobed, the attachment to the host's root being small if not minute. The general shape of the haustorium thus becomes broad above and narrow below : the case in *Santalum* is the reverse, some of the oldest and largest haustoria collected being smooth and conical or limpet-shaped.

The development of the young haustorium is very similar to that in both the haustoria thus far considered, but when the nucleus is formed, its cells are sharply separated off from those above, the latter being elongated in a direction at right angles to the axis. When entrance is being effected, the cells of the upper part of the nucleus assume a striking appearance. They become much enlarged, develop dense, granular protoplasm and large nuclei and nucleoli—assume in fact the structure of glandular cells. The gland proper is small and slit-like and there is no duct. It thus would appear that, in *Cansjera,* the whole of the nucleus forms a gland, the so-called "gland" perhaps acting as its lumen and duct. In *Santalum,* the cells of the upper part of the nucleus do not take on any peculiar form and, although sharply marked off from those above, remain small. The gland, on the other hand, is well

developed. It is divided into an upper, broader part with distinct lumen and a lower, narrow portion, while the tissues between it and the host's root are traversed by a distinct duct.

Cork is much commoner in *Cansjera* haustoria and lenticels are frequent. A layer of tissue below the epidermis or cork remains smaller celled and has peculiar contents which persist in the form of drops. Such a hypodermal tissue is absent from *Santalum*. Sclerotic pitted cells are found in the cortex. In place of the calcium oxalate crystals found in *Santalum* there are similar crystals of calcium carbonate.

The cortical folds soon cease to grow round the root of the host and become thickened instead. They are thus usually short and thick, and do not envelope much of the host's circumference. In advanced stages the folds are small and functionless. The folds in *Santalum* continue to grow round the root attacked for a considerable time and distance, and there is no secondary growth in thickness. In *Cansjera* a small group of cells in the end of the fold become thick-walled, pitted and lignified: there is nothing of the kind in *Santalum*. The collapsed layers terminate upwards more or less as in *Santalum*, but, downwards, they end at a point half-way between the edge of the fold and the side of the sucker. Taking into consideration the shortness of the folds, the result of this is that the collapsed layers are much more erect and frequently vertical. With secondary thickening they soon become vertical, if not so before, then converge downwards and finally lie almost in one line pointing towards each other. There is a similar movement in *Santalum*, but, even in the extreme case figured in *Sant. I*, Plate IX, the collapsed layers are far from this position. These layers in old *Cansjera* haustoria dwindle into insignificance.

The inner cortex is separated in *Cansjera* into two more or less distinct parts at the time of penetration: an upper and outer where the cells become filled with starch and remain equal-sided, and an inner and lower where the cells are protoplasmic, become elongated and take part in the formation of

the sucker. It is probable that something of this kind also takes place in *Santalum*, but at present it has only been noted that a few of the cortical cells near the sucker are dragged in with the penetrating nucleus. In *Olax* a similar subdivision into starchy and protoplasmic cells takes place, but these cells belong to the cortex and nucleus respectively.

An endodermis is very clearly seen in most haustoria. It accompanies the branch of bundles from the mother root and is found round each of its subdivisions in the transitional region, and ceases at the interrupted zone. The latter zone is especially clear in *Cansjera* and is evidently centrifugal in its development.

The activity of the cambium varies in different parts of the haustorium. In the axis it soon ceases to form wood, but for a long time forms layers of cells outwards which may be regarded as secondary cortex. In the vascular loop a great development of xylem takes place, with the result that the vascular strands assume a characteristic and peculiar shape. The older haustoria are chiefly composed of xylem, and it is chiefly due to its development that the form of such old haustoria is turbinate. In *Santalum*, although there is a similar development of secondary cortex, the formation of wood takes place equally in the axis and the loop.

The sucker is narrow in *Cansjera* and little lobed, resembling the cortical folds in this limited growth. An abundance of yellow "gummy" substance is found in different parts of the haustorium from the decomposition of its cells. This extends to the collapsed layers whose decay is seen to be centripetal and sometimes complete. Such decayed tissues are frequently surrounded by meristematic divisions in the neighbouring cells. A brilliant cap of clear yellow substance is found over the end of each of the host's wings. This formation of yellow substance and internal meristems is much rarer in *Santalum*.

BOTANY SCHOOL, CAMBRIDGE;
30*th December*, 1907.

APPENDIX.

List of Plants attacked by *Cansjera*, whose roots have been examined in the preparation of this paper.

Abrus precatorius.[2]
Acalypha paniculata.
Aerua lanata.
Alangium Lamarckii.[2]
Argyreia speciosa.
Azima tetracantha.
Barleria buxifolia.
Calophanes vagans.
Cansjera Rheedii.[2]
Capparis horrida.
,, zeylanica.[2]
Carissa spinarum.
Celastrus paniculata.
Commelina suffruticosa.
Curculigo orchioides.
Diospyros Chloroxylon.
Grewia hirsuta.
Hardwickia binata.
Helicteres Isora.
Hemidesmus indicus.[3]
Hippocratea obtusifolia.
Ichnocarpus frutescens.
Jasminum auriculatum
Lantana Camara.
Mallotus distans.
Pavetta indica.
Phyllanthus debilis.
Plumbago rosea.
Premna tomentosa.
Pupalia atropurpurea.
Randia malabarica.
Santalum album.
Sida humilis.
Streblus asper.
Strobilanthes consanguineus.
Strychnos Nux-Vomica.
Tamarindus indicus.
Toddalea aculeata.
Vernonia travancorica.
Webera corymbosa.[2]
Zizyphus Oenoplia.
,, Xylopyrus.
And a few others.

2, 3 The figures appended signify the number of localities from which the collections were made. The three regions examined were over 500 miles from each other. In each of these *Hemidesmus indicus* and in two of them *Abrus precatorius*, etc., were not only associates but actually hosts.

[illegible] haustoria (Dancyna Dancyi with young haustoria [illegible]
[illegible] and magnified). The rootlets are practically bare of
[illegible] but the young haustoria are somewhat thickly coated
with them (*h*, *h*).

[illegible]

Fig. 3. Older haustoria (natural size and magnified). These are becoming
[illegible] warty and are covered with lenticels.

[illegible] : [illegible] haustoria (natural size. No. 5 also magni-
fied). The sucker is shown in 5 and 6 and, in the latter case,
a piece of the host's bark is attached. The haustoria are
seen to be much broader above than at the point of their
attachment.

Fig. 6. An early stage of haustorial development, cut transversely. (Nut
with the microtome, stained with Delafield's hæmatoxylin
and mounted in Canada balsam. The haustorium is fixed
[illegible]
as a median, oval area. *a*, part of the procambial strand
magnified further : *b* and *c*, the surface of attachment to the
host's bark.

Plate I.

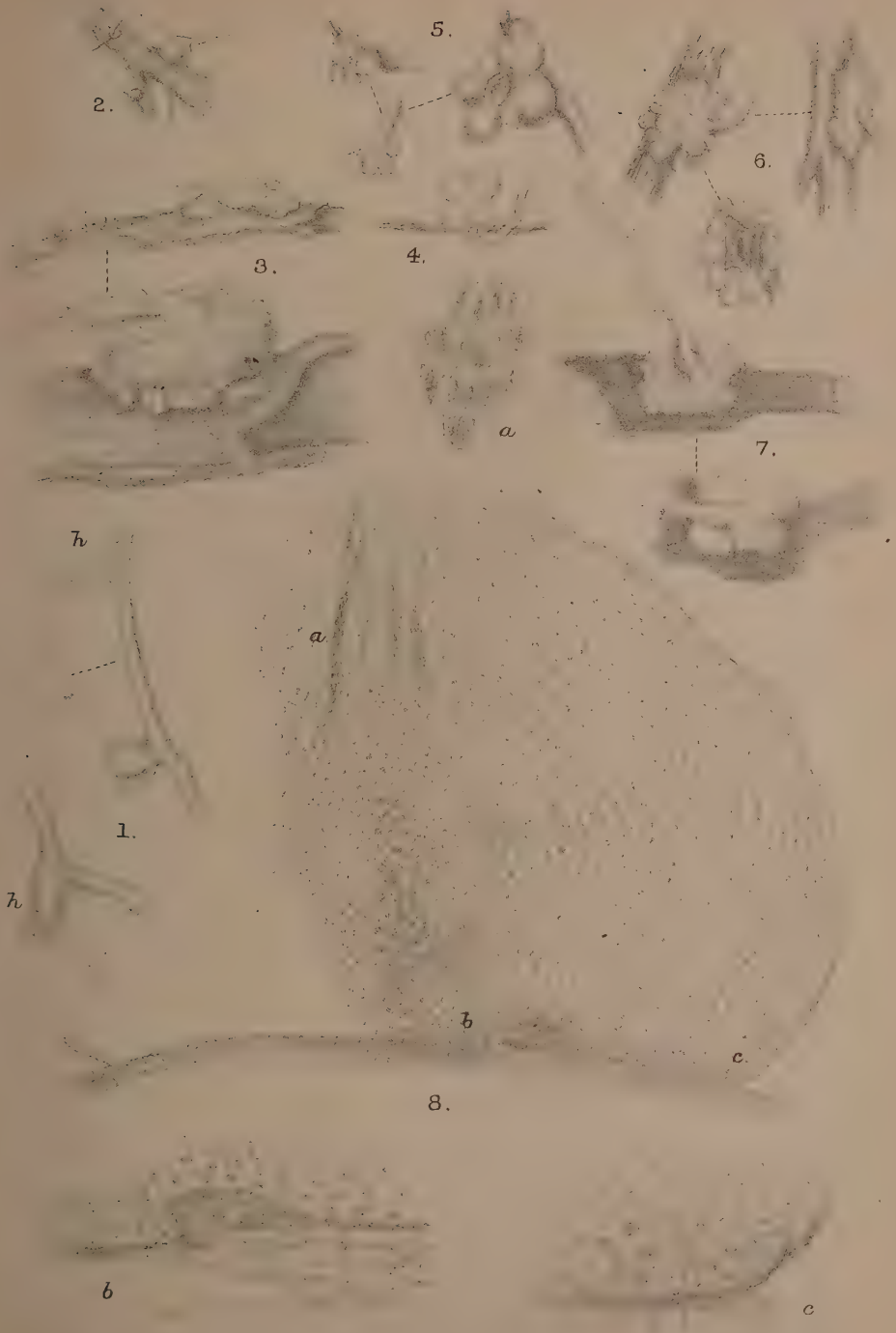
Fig. 1. Terminal rootlets of *Cansjera Rheedii* with young haustoria (natural size and magnified). The rootlets are practically bare of root hairs, but the young haustoria are somewhat thickly coated with them (*h*, *h*).

Fig. 2. Young haustoria (natural size). Their surface is still smooth.

Fig. 3. Older haustoria (natural size and magnified). These are becoming wrinkled and warty and are covered with lenticels.

Figs. 4-7. Old, irregularly-lobed haustoria (natural size. No. 5 also magnified). The sucker is shown in 5 and 6 and, in the latter case, a piece of the host's bark is attached. The haustoria are seen to be much broader above than at the point of their attachment.

Fig. 8. An early stage of haustorial development, cut transversely. Cut with the microtome, stained with Delafield's hæmatoxylin and mounted in Canada balsam. The haustorium is fixed on a root of *Abrus precatorius*. The nucleus is developing as a median, oval area. *a*, part of the procambial strand magnified further : *b* and *c*, the surface of attachment to the host's bark.



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in haustorial development.

being taken on a root of [illegible]
mounted in dilute glycerine. The gland is appearing as a

in the text, further enlarged.

[illegible] cium is fixed to a root of Cyperus sejunctus.
[illegible] between medens and cortex is clear, as als
vascular loop and the collapsed larvis. The enlarged drawin
of the lumen of the gland (a) shows that the secreting cells a
behaving exactly as in Santalum. The cell contents of b
cortex are not inserted in the drawing. a, gland; bb, colla

PLATE II.

Fig. 1. A second stage in haustorial development, this haustorium also being fixed on a root of *Abrus precatorius*. Cut by hand and mounted in dilute glycerine. The gland is appearing as a median shadow, *e* ; *a* to *g* show the various tissues as described in the text, further enlarged.

Fig. 2. A further stage in development in which the gland is formed. The haustorium is fixed to a root of *Capparis zeylanica*. The distinction between nucleus and cortex is clear, as also the vascular loop and the collapsed layers. The enlarged drawing of the lumen of the gland (*a*) shows that the secreting cells are behaving exactly as in *Santalum*. The cell contents of the cortex are not inserted in the drawing. *a*, gland : *bb*, collapsed layer.

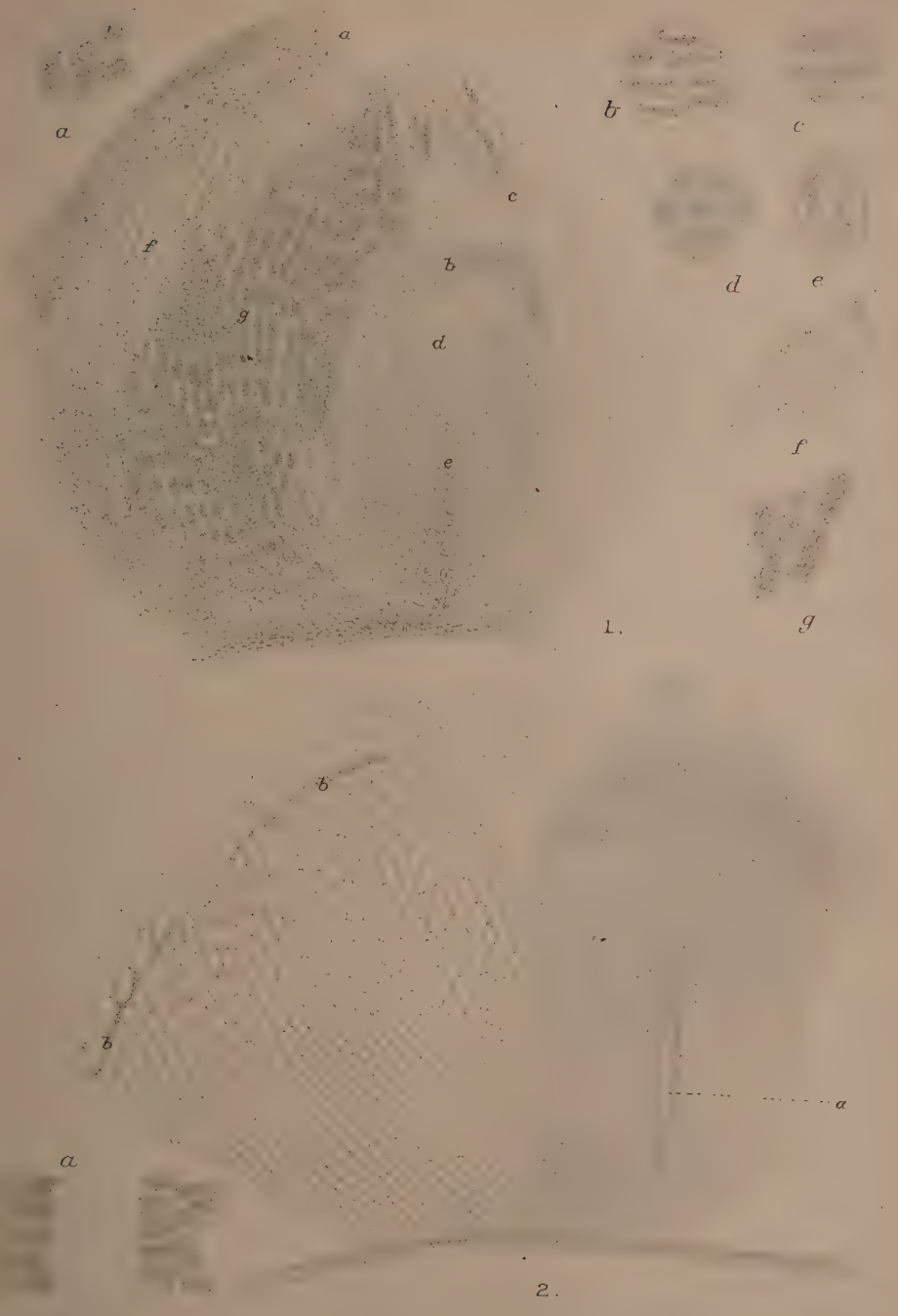

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Plate III.

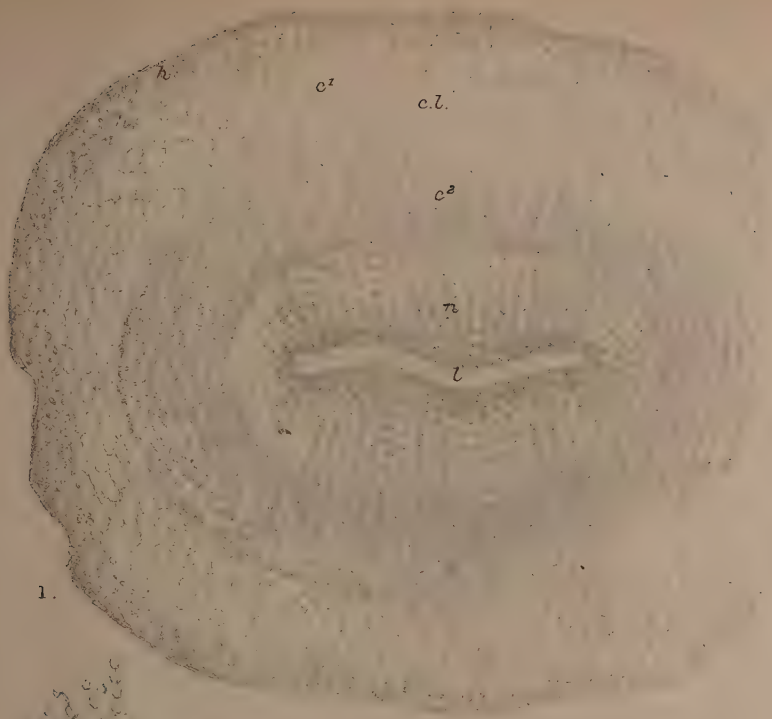
Plate III.

Fig. 1. Horizontal section through a young haustorium fixed on a root of *Hemidesmus indicus*. The hypoderm (*h*), outer and inner cortex and collapsed layers (*c.l.*) separating them, clear (c^1) and starchy (c^2) cells of the cortex, protoplasmic cells of the nucleus (*n*), secreting cells and lumen of the gland (*l*) are clearly shown.

Fig. 2. The secreting cells from another gland, showing the rods of mucilaginous substance extruded into the lumen of the gland (cf. *Sant. I*, fig. 25).

Fig. 3. Transverse section through a diseased haustorium fixed on a root of *Abrus precatorius*. The stage is somewhat older than the last two, as shown by the gland trace (*a*) in the middle. The tissues of the nucleus are decomposed down one side and the cavity thus formed is lined with yellow substance. *a-c* show the parts magnified. *c*, lignified pitted cells.

Fig. 4. A portion of another haustorium of about the same age, also found on *Abrus precatorius*, showing the cells of the sucker in contact with the wood of the vascular cylinder.



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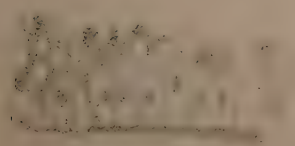

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Plate IV.

Transverse section through a haustorium in the act of penetrating a small root of *Abrus precatorius*, the diameter of the haustorium being one-sixteenth of an inch. A microtome section, stained with hæmatoxylin and mounted in Canada balsam. The interest centres in the nucleus (*d*). The upper part of this shows cells greatly enlarged and furnished with granular protoplasm, great nuclei and nucleoli. At d^1 cells of a slightly younger haustorium are figured. The lower part of the nucleus merges into the sucker and contains the gland which is narrow and duct-like (*i*). At *j* the thick-walled, lignified, pitted cells are seen in the thickness of the end of the cortical fold. For the description of this plate see paragraph 6 of the text. The smaller drawings, with the exception of *d'*, are enlargements of different parts of the haustorium.

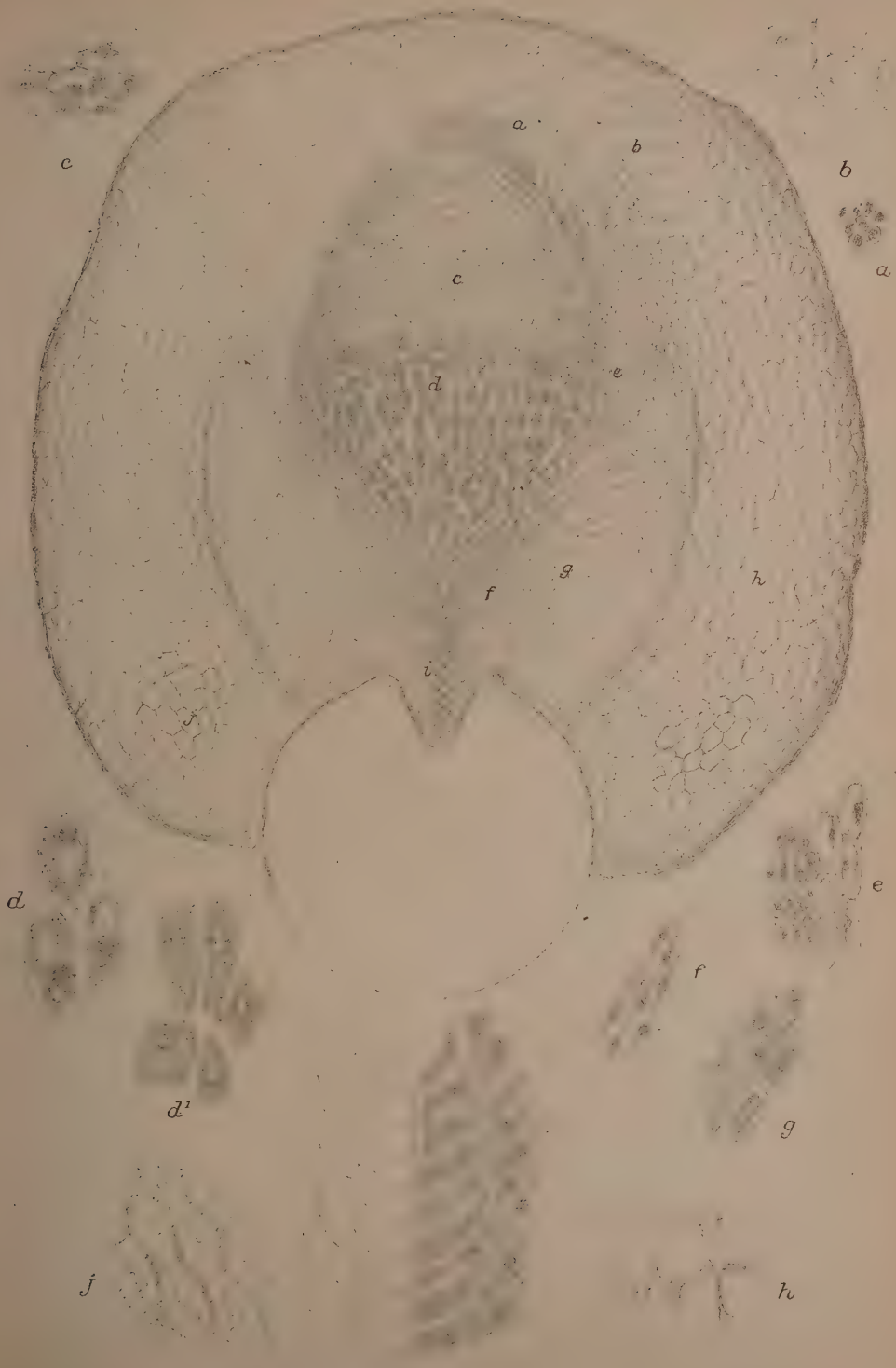

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Plate V.

Fig. 1. Transverse section through a haustorium which has entered a root of *Pavetta indica*. The parts are still young and no vessels are formed. The nuclear cells are more vacuolated and less regular (*a*). At (a^1) the cells from a slightly older nucleus are shown. In the inner cortex there is a sharp distinction between the starchy (*b*) and protoplasmic cells (*c*), the latter being elongated and taking part in the formation of the sucker. Secondary thickening is taking place in the cortical fold (*d*).

Fig. 2. A haustorium fixed on a root of *Santalum album*. This may be taken as the type of the mature organ, as the vascular connection between host and haustorium is complete and the various tissues are becoming emptied of their contents. This is especially noteworthy in the breaking down of the cells at the top of the nucleus (*a*). Note also the endodermis (*e*) and the medullary rays (*m. r.*) in the transitional region, the cambium (*c*), collapsed layers and low-lying lacunæ (*lac*) inside them; also the bright cap of transparent yellow substance (*x*) at the end of each of the host's cortical wings. The structure of this is shown in fig. 4 of Plate VII. *b*, hypoderm.

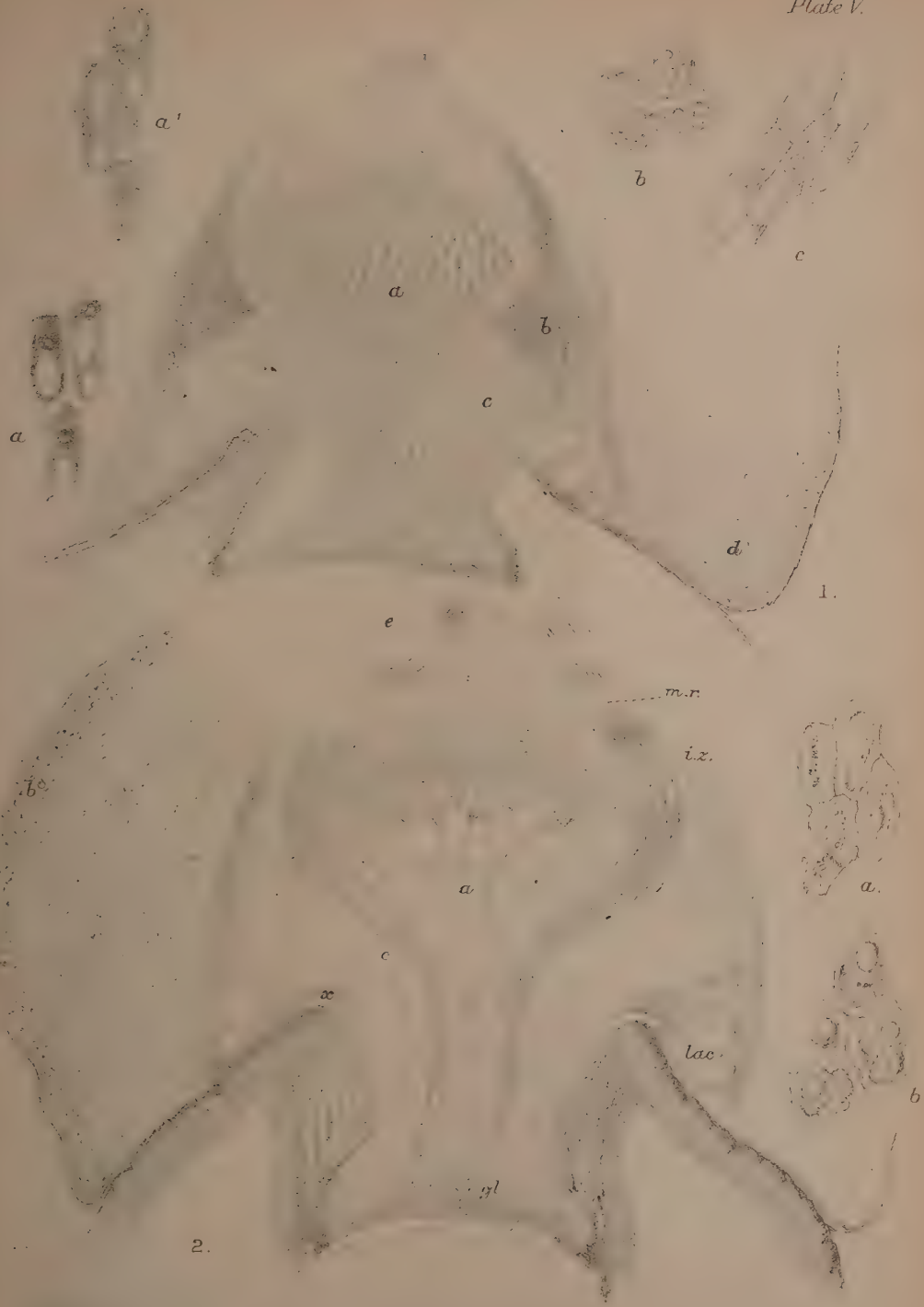

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Plate VI.

Plate VI.

Fig. 1. Part of the periphery of a haustorium attacking a root of *Hemidesmus indicus*. In this the layer of cork is seen, the hypoderm (*h*) with contents collected into drops, the starchy cells and the thick-walled, pitted, sclerotic cells of the cortex (*scl*).

Fig. 2. Masses of tabular crystals of calcium carbonate from the inner cortex of a haustorium on *Lantana Camara*. The cell contents in the cell on the right hand side (*x*) show the delicate reticulation in a crystal cell which has lain for some months in dilute glycerine and from which the crystals have been dissolved.

Fig. 3. Mulberry-like masses of calcium carbonate from the cortex of a haustorium on *Capparis horrida*.

Fig. 4. Radiating crystal masses found in the outer cortex of another such haustorium.

Fig. 5. Thick-walled cortical cells as in fig. 1, from a haustorium on *Vernonia travancorica*. In one of these a mass of calcium carbonate crystals is to be seen.

Fig. 6. A section through a part of a haustorium on a root of *Toddalea aculeata*. Note the masses of calcium carbonate crystals in the usual place, in the elongating part of the inner cortex. Also note that the collapsed layer (*c.l.*) is broken down to a uniform mass of yellow substance and that this is continuous right down round the end of the wing of the host's cortex to the angle opposite the edge of the sucker lobe (*l*). *lac*, lacunar region.

Fig. 7. A section through the cortical fold of a haustorium on *Capparis horrida*. The darker cells (*d*) are lignified and thickened and are not only found in the end of the fold but run up beneath the hypoderm for a considerable distance (*d,d'*). An enlarged drawing of such cells is seen in fig. 5 of Plate VII. *lac*, lacunar region.

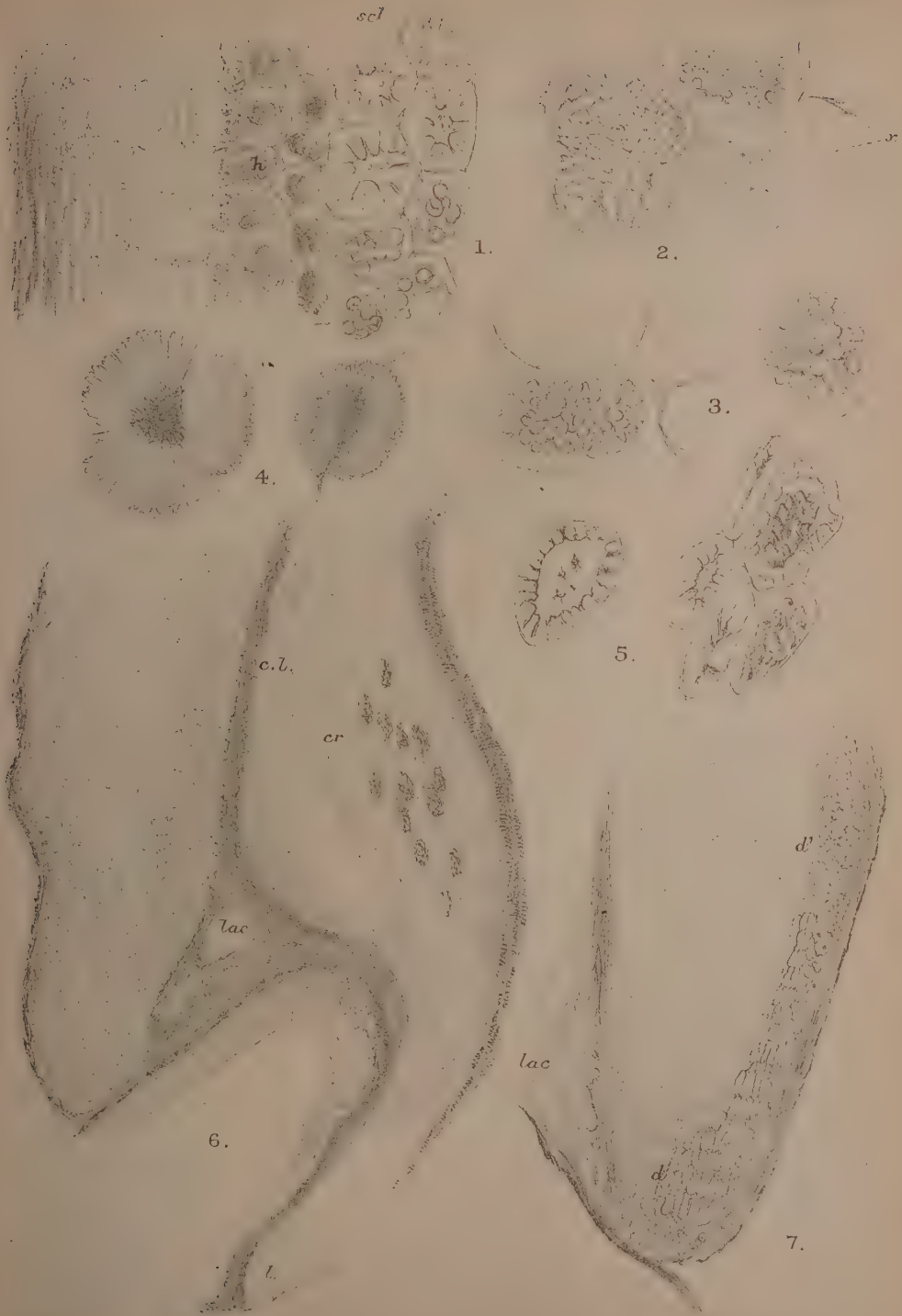

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PLATE VII.

Fig. 1. One side of the vascular loop in a haustorium attached to a root of *Viscum Loranthi*. This shows one of the bundles in the transitional region with its endodermis (*e*), the interrupted zone (*i.z.*) and the vascular loop below it, the upper ending of the collapsed layer (*c.l.*) and the upper part of the disintegrated nucleus (*n*).

Fig. 2. Part of the same further magnified.

row (*o*) retain their white walls and are indistinguishable from those of the main axis. All the rest are yellow.

Fig. 4. One of the caps of clear yellow substance shown at the end of the host's cortical wings (as at *x* in fig. 2 of Plate [illegible]) further magnified. It is evident that this clear yellow substance is made up of broken-down cells of the haustorium, apparently compressed by the host's bark (*b*) below.

Fig. 5. A portion of the haustorium shown in fig. [illegible] of Plate [illegible] further magnified.

Plate VII.

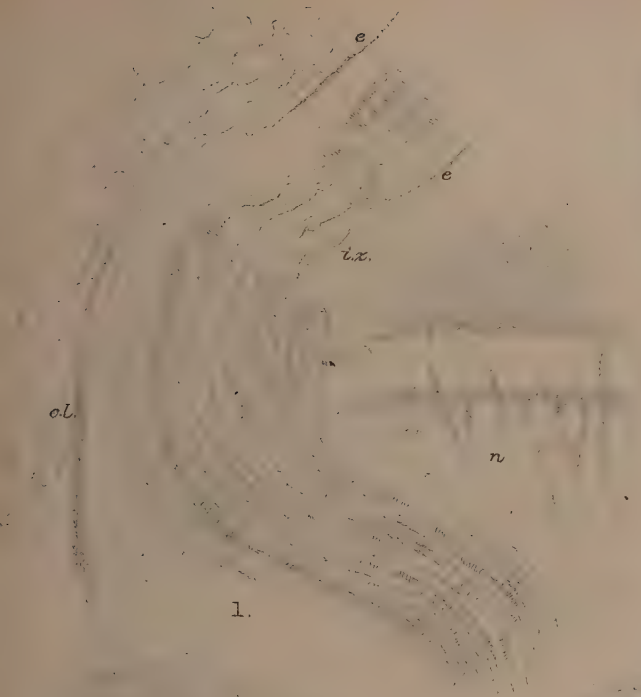
Fig. 1. One side of the vascular loop in a haustorium attached to a root of *Alangium Lamarckii*. This shows one of the bundles in the transitional region with its endodermis (*e*), the interrupted zone (*i.z.*) and the vascular loop below it, the upper ending of the collapsed layer (*c.l.*) and the upper part of the disintegrated nucleus (*n*).

Fig. 2. Part of the same further magnified. The bast is shown under the endodermis (*e*) and contains the callus-plate of a sieve tube (*s.t.*). The isolated rows of vessels in the interrupted zone have lost their markings excepting a few in the outermost vessels, and have become filled with a yellow gummy mass. Their downward branching into white-walled, pitted vessels is well seen, as well as the thin-walled parenchyma between them.

Fig. 3. Part of the interrupted zone in a haustorium fixed on a root of *Capparis horrida*. Here the disintegration of the vessels has proceeded centrifugally and only the outer ones retain any of their markings. The vessels in the outer, latest formed row (*o*) retain their white walls and are indistinguishable from those of the main axis. All the rest are yellow.

Fig. 4. One of the caps of clear yellow substance shown at the end of the host's cortical wings (as at *x* in fig. 2 of Plate V) further magnified. It is evident that this clear yellow substance is made up of broken-down cells of the haustorium, apparently compressed by the host's bark (*b*) below.

Fig. 5. A portion of the haustorium shown in fig. 7 of Plate VI, further magnified. Note the cork, hypoderm (*h*) and the lignified, pitted cells below it.



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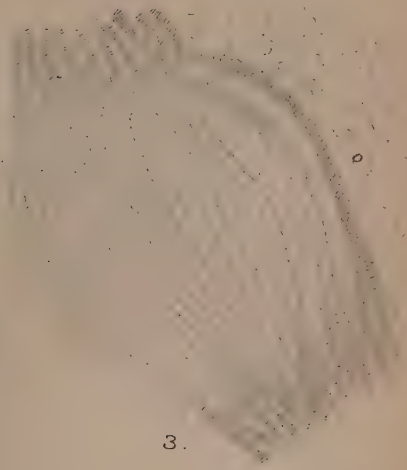

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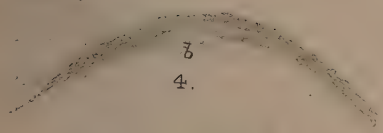

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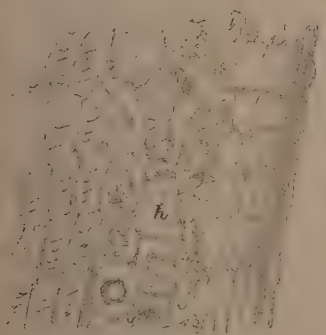

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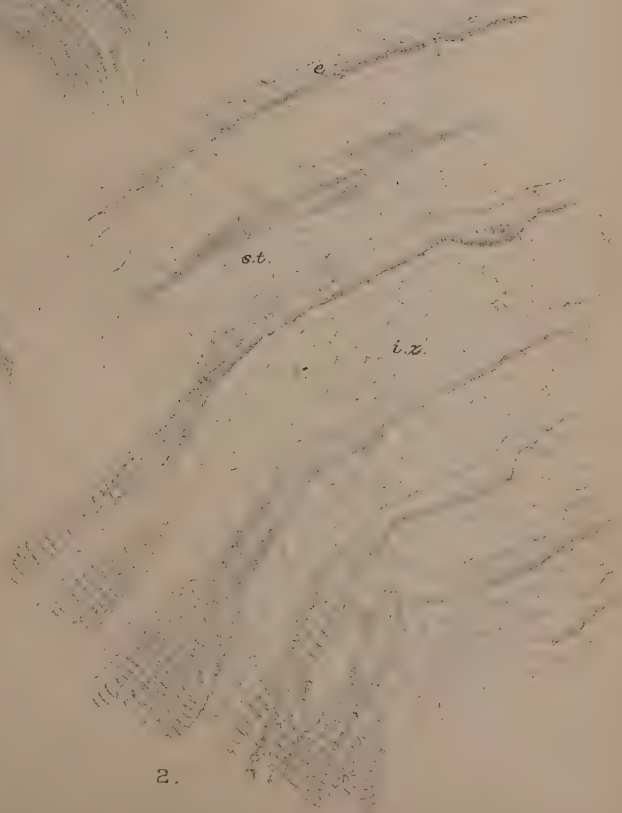

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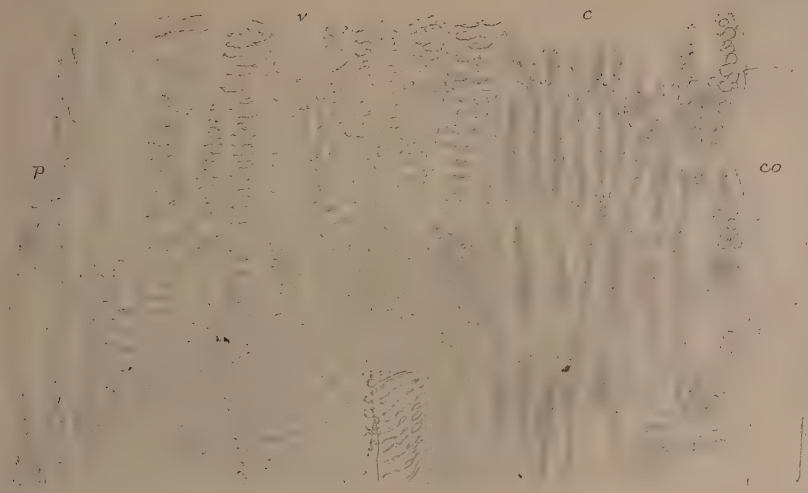
Plate VIII.

Fig. 1. A portion of the axial vascular strand in a haustorium attacking a root of *Plumbago rosea*. Proceeding from left to right, note, in succession, the cells of the pith with delicate protoplasmic sacs (*p*), the vessels (*v*) with long, irregular pits, the cambium (*c*) of nucleated protoplasm, and the starch-filled cells of the inner cortex (*co*). The contents of the outermost rows of the latter are not drawn. There is no trace of bast.

Figs. 2 and 3. The upper part of the axis of a haustorium on *Alangium Lamarckii*. Note the square vessels on the inner side (*sq*). In fig. 3 the pits are drawn on only one of the ordinary vessels (*v*) whose outlines are shown. They are altogether similar to those in fig. 1.

Figs. 4 and 5. Small portions of the vascular strands in different parts of the same haustorium on an unknown root. Fig. 4 is drawn from the mother root of the haustorium itself and shows the broad vessels with small, regular, oval pits and a sieve-tube (*s.t.*) in the bast. Fig. 5 shows the narrow elements of the sucker with irregular, long pits, frequently extending right across the vessels.



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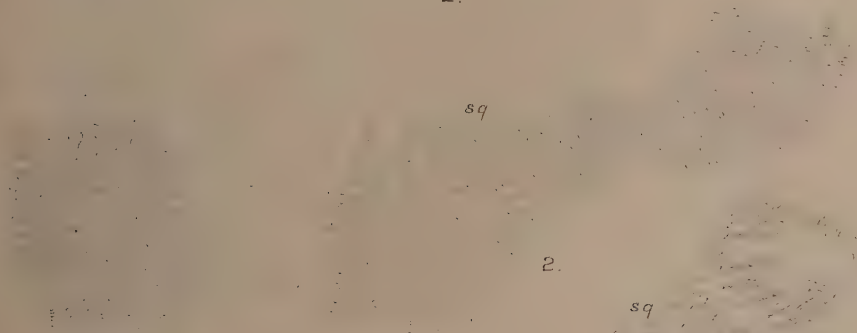

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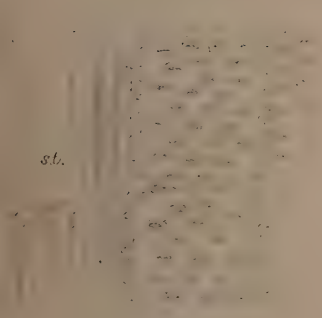

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Plate IX.

Fig. 1. An older haustorium fixed on *Argyreia speciosa*. The vascular system has undergone considerable growth in thickness. Note the place where most thickening takes place (*x*), just below the interrupted zone. The bundle from the mother root (*m r.*) is seen, as also its two divisions in the transitional region. A dark yellow mass (*b*) marks the upper limit of the nucleus. The cambium in the axis, while forming little secondary wood, has given rise to a series of rows of cells (*a*) simulating a secondary cortex. Some of these cells are enlarged at *a* and do not at all present the appearance of bast. The inner cortex is charged with calcium carbonate crystals (*cr*) and the collapsed layers (*c.l.*) are small and converge downwards.

Figs. 2 and 3. Thyloses from an invaded root of *Vernonia travancorica* showing calcium oxalate crystals and thick-walled, pitted cells inside them.

Fig. 4 A thylose from the same root of *Argyreia speciosa* with thickened and pitted cells inside it.

Fig. 5. A very old haustorium attached to a root of *Cansjera Rheedii*, cut in the middle and therefore appearing to be more regular than most (see figs. 4-7 of Plate I, where haustoria of the same age are shown). The haustorium now consists practically of only the vascular system. The root attached has been broken up and the point of attachment is minute. The collapsed layers (*c.l.*) are still visible but quite inconspicuous : they are so far disturbed by the secondary growth in thickness that they are almost in the same horizontal line. Masses of calcium carbonate crystals (*cr*) are found in both inner and outer cortex, the whole of this tissue now assuming the appearance of bark. The secondary cortex (co^2), formed by the cambium outwards, is broad and clear of contents. The greatest development of the xylem is in the upper part of the vascular loop (*x*) and this dominates the form of the haustorium which is now turbinate. The interrupted zone (*i.z.*) is bridged over by about forty strands of decomposed vessels. The upper end of the nucleus (*n*) is still discernible and the cells of the ground tissue above it are charged with crystals.

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Part of the sinker, showing the cells in the act of
attacking the root of Plumbago rosea. Th
drawn in some of the cells. Strands of vessels are formed
sucker opposite to the vessels in the host's xylem, an
contents than the rest (pp). The cells at the side of the suc
(w) have ceased actively secreting and are cut off by
collapsed layer (c.l.) from the rest of the haustorium. Cork
(ck) is formed opposite to these in the host's wing.

A similar portion of an older haustorium attached to a root of
Sandalum album. The strand of vessels (v) in the haustoriu
is formed opposite to the vessels in the host's root.
the side of the sucker (w) are cut off by a co
[illegible] they are protruded and crammed with

[illegible] the sucker, this layer is situated out
formed by the breaking down of the cells of
rather out, the cells of the host evidently take part.

haustorium is composed of glandular
continued to the cells lining the lumen of the p
specimen, which is unique among those examined, is
met with in the haustoria of Santalum album on
radicum (Sprat. I. fig. 3d). Some of the cells are radi
and b and show the position of the glairy secretion.
cortical.

A haustorium attacking a root of Acacia horrida. The
this root is arranged in concentric bands sepa
walled parenchyma (p). A black "secretion
sucker from the host, but the section is in
showing that this layer is absent where the p
is taking place (w). The point of junction of
systems of host and haustorium is drawn
scale at c.

Plate X.

Fig. 1. Part of the sucker, including the edge of one lobe, in a haustorium attacking the root of *Plumbago rosea*. The contents are only drawn in some of the cells. Strands of vessels are formed in the sucker opposite to the vessels in the host's xylem, and the cells adjoining these vessels are fuller of protoplasmic contents than the rest (*pp*). The cells at the side of the sucker (*a*) have ceased actively secreting and are cut off by a collapsed layer (*c.l.*) from the rest of the haustorium. Cork (*ck*) is formed opposite to these in the host's wing.

Fig. 2. A similar portion of an older haustorium attached to a root of *Santalum album*. The strand of vessels (*v*) in the haustorium is not formed opposite to the vessels in the host's root. The cells at the side of the sucker (*a*) are cut off by a collapsed layer (*c.l.*), and they are moribund and crammed with starch. Between these cells and the inside of the wing of the host's bark there extends a broad layer of clear yellow substance (*b*). Near the sucker, this layer is striated and is apparently formed by the breaking down of the cells of the sucker: further out, the cells of the host evidently take part. The cells of the host's wood are filled with dark brown substance.

Fig. 3. A young haustorium on *Abrus precatorius*, which has successfully entered the host's root and yet has withdrawn itself from the woody cylinder. The whole surface (*a*) of this part of the haustorium is composed of glandular cells filled with typical, dense, granular protoplasm, a structure usually confined to the cells lining the lumen of the gland. This specimen, which is unique among those examined, recalls those met with in the haustoria of *Santalum album* on *Pterolobium indicum* (*Sant. I*, fig. 34). Some of the cells are enlarged at *a* and *b* and show the position of the glairy secretion below the cuticle.

Fig. 4. A haustorium attacking a root of *Aerua lanata*. The xylem *x* in this root is arranged in concentric bands separated by thin-walled parenchyma (*p*). A black "secretion" separates the sucker from the host, but the section is interesting in showing that this layer is absent where the passage of fluids is taking place (*a*). The point of junction of the vascular systems of host and haustorium is drawn on a larger scale at *a*.

Plate X.

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PLATE XI.

Fig. 1. An attack of Cuscuta upon a root of Capparis horrida. A portion of the sucker and the end of one of the host's cortical wings are shown. The cells of the wing are completely isolated from the rest of the host's tissues by a thick layer of cork (ck), and yet they are crammed with starch while the rest of the root has little or none. In the tissues are further magnified. The cells at the side of the sucker (x) are cut off by a collapsed layer and are filled with minutely granular starch (the original contents apparently suffering fragmentation). The cells of the wing are dead and browned but filled with clear and large starch grains.

Fig. 2. The sucker of a haustorium imbedded in a root of Capparis horrida. The parts within the dotted lines are full of starch (st) and this substance is absent from the rest of the section. Starch, it will be seen, is only deposited where the layer of secretion is formed, that is, presumably, where the passage of fluids has ceased. The remains of a former gland (gl) are seen.

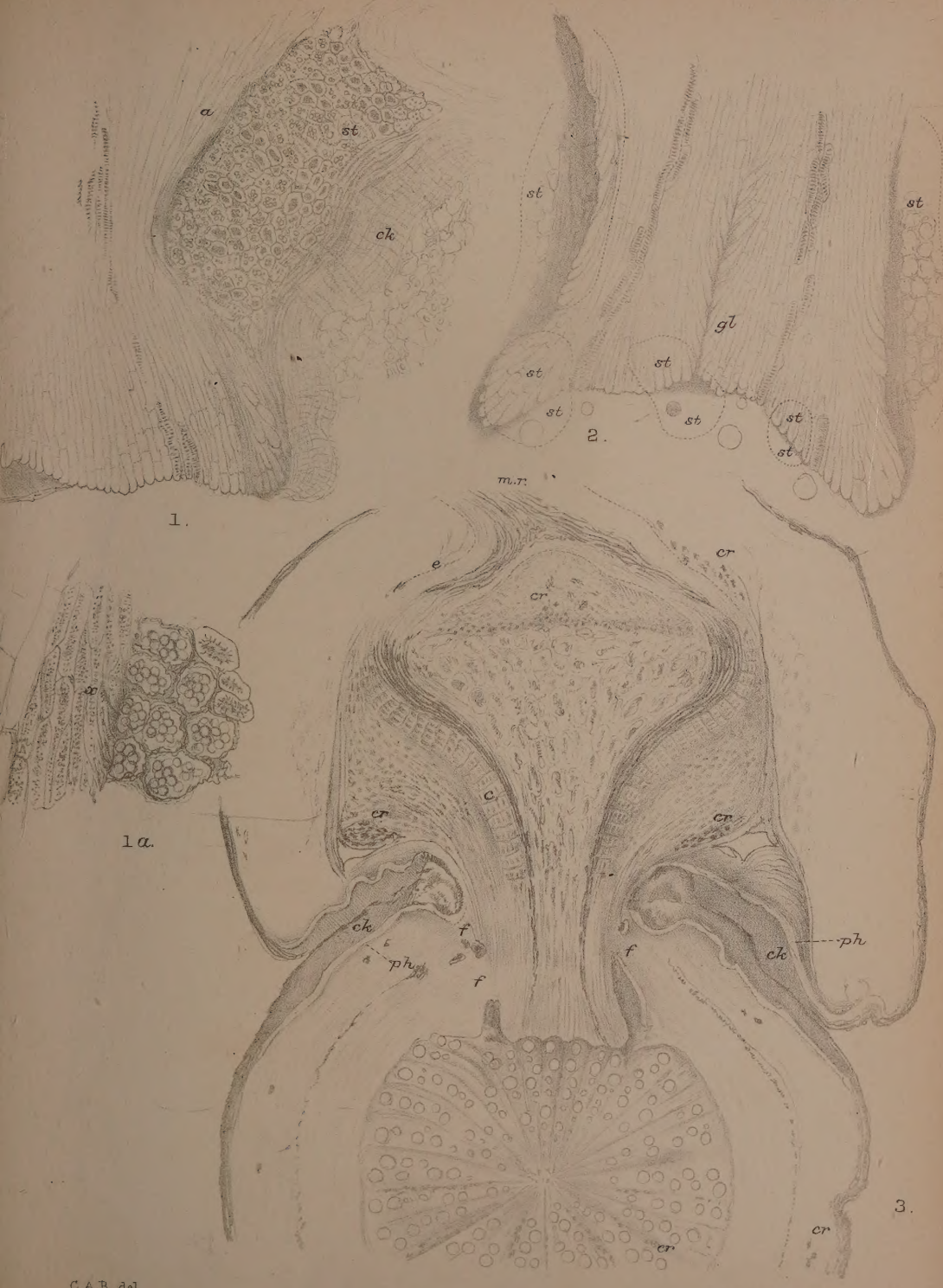
Fig. 3. A haustorium of Cuscuta Meadii penetrating another Cuscuta root. The haustorium which, in many respects, is typical, has fused in various places (f) with the host's tissues. Note the bundle from the mother root (mr.) with its bast and endodermis (e). These are absent in the haustorium, but a thick layer of cambiform tissue (c) is met with. The distribution of the masses of calcium carbonate crystals (cr) in host and haustorium is instructive. Broad bands of cork are formed where the cortical folds are in contact with the host's bark, the discoloured portions being old cork (ck) and the white lines young cork and phellogen (ph).

Plate XI.

Fig. 1. An attack of *Cansjera* upon a root of *Capparis horrida*. A portion of the sucker and the end of one of the host's cortical wings are shown. The cells of the wing are completely isolated from the rest of the host's tissues by a thick layer of cork (*ck*), and yet they are crammed with starch while the rest of the root has little or none. In 1*a* the tissues are further magnified. The cells at the side of the sucker (*x*) are cut off by a collapsed layer and are filled with minutely granular starch (the original contents apparently suffering fragmentation). The cells of the wing are dead and browned but filled with clear and large starch grains.

Fig. 2. The sucker of a haustorium imbedded in a root of *Capparis horrida*. The parts within the dotted lines are full of starch (*st*) and this substance is absent from the rest of the section. Starch, it will be seen, is only deposited where the layer of secretion is formed, that is, presumably, where the passage of fluids has ceased. The remains of a former gland (*gl*) are seen.

Fig. 3. A haustorium of *Cansjera Rheedii* penetrating another *Cansjera* root. The haustorium which, in many respects, is typical, has fused in various places (*f*) with the host's tissues. Note the bundle from the mother root (*m.r.*) with its bast and endodermis (*e*). These are absent in the haustorium, but a thick layer of cambiform tissue (*c*) is met with. The distribution of the masses of calcium carbonate crystals (*cr*) in host and haustorium is instructive. Broad bands of cork are formed where the cortical folds are in contact with the host's bark, the discoloured portions being old cork (*ck*) and the white lines young cork and phellogen (*ph*).



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